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Abstract

Animals often encounter novel environments, both naturally and due to human activities. Translocations are conservation actions that introduce animals to new habitats. Animals' behaviors post-release can provide useful tools for assessing translocations' outcomes. In addition, translocations provide extraordinary opportunities for studying basic questions about the animals' behavior in novel settings that are relevant to natural life history stages, such as dispersal. Here I present the outcome of the largest African elephant (*Loxodonta africana*) translocation.

In Chapter One I examine the settlement process of the translocated elephants. I show that both males and females left the release site and returned home. In addition, the exploration patterns of the elephants remaining at the release site varied greatly among individuals, and the degree to which individuals explored their new home negatively correlated with their approach distance to a human observer. In Chapter Two I provide details on the translocated elephants' demographics, behavior, and physiology, and compare them to the local resident population. The translocated elephants' behavior and stress hormones converged with those of the local population. However, the translocated elephants' death rates were higher than those of the locals and their body condition was poorer. These two first chapters use behavior to assess the outcomes of the translocation and to provide recommendations for future management actions.

In Chapter Three I address basic questions in animal behavior by examining the social response of the translocated elephants to their new home. The translocated elephants preferred interacting with more conspecifics upon arrival to their new home than later, when the habitat became familiar to them, suggesting there are added benefits to sociality when a habitat is unfamiliar. Furthermore, I show that the translocated elephants preferred interacting with familiar conspecifics and not with the local residents. This social segregation dissolved over time, suggesting that elephants are able to integrate into an existing social setting.

This study melds applied and basic research in animal behavior. It is the first to report on the outcomes of an elephant translocation that involves both family groups and adult males, and it successfully utilizes management actions to explore animals' behavior.

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Preface

Translocations are often used in wildlife conservation and management actions. However, very few translocations are successful (Griffith et al. 1989; Fischer and Lindenmayer 2000), begging for investigation into the factors influencing translocation outcomes. Behavior serves as an interface between animals and their environments. The behavior of translocated animals can determine their ability to survive at the release site and can provide useful tools for assessing the outcome of these conservation actions (Bremner-Harrison et al. 2004; Shier and Owings 2006). In addition, conservation actions can provide extraordinary experimental manipulations for studying basic scientific questions about the behavior of animals that may be relevant to certain stages of their life histories (Sarrazin and Barbault 1996). Thus, both applied conservation and the discipline of animal behavior can benefit greatly from an information exchange.

Here I present the outcome of the largest ever African elephant (*Loxodonta africana*) translocation. This is the first study to provide a detailed report on the demographics, behavior, and physiology of an elephant translocation that involves both family groups and adult males. In the first two chapters I use techniques from animal behavior to assess the outcome of the translocation and provide recommendations for future management actions. In my third chapter I address basic questions in animal behavior by examining the social response of the elephants to their new home.

When animals arrive at a novel environment they can reject it and leave, or they can remain and explore their new surroundings in search of a suitable place in which to settle. Understanding what factors lead animals to reject or accept a release site and how life history may influence animals' behavior at their new home can be useful for improving conservation actions (Stamps and Swaisgood 2006). In Chapter One I show that although both male and female translocated elephants left the release site and homed back to the source site, most translocated elephants remained at the release site and exhibited great individual variation in their exploration patterns of their new home. Since the exploration process entails both benefits and costs (Stamps 2001), it is vital to understand the factors leading to individual variation in this behavior. The degree to which translocated elephants explored the novel habitat negatively correlated with their approach distance to a human observer. If we are interested in influencing the behavioral make-up of translocated populations, we can use distance to observers as a predictor for exploratory behavior and as a tool for deciding which individuals to target in future translocations.

Behavioral and physiological measures can provide a quick assessment of a translocation's outcome that is valuable when dealing with long-lived animals or when rapid management decisions are called for. Still, physiology and behavior are only seldom used for assessing management actions (Wikelski and Cooke 2006; Teixeira et al. 2007). In Chapter Two I provide information about the demographics, physiology, and behavior of the translocated elephants. I compare these biological measures to the local elephant population at the release site, to better understand the outcome of the translocation. I found that the behavior and stress hormone levels of the translocated elephants converged with those of the local population over time (within one year), and that the translocated elephants used habitat that is similar to the habitat at their source site. However, body condition and survival rate of the translocated elephants were poorer than those of the local population. Thus, in some aspects, the translocated elephants acclimated to their new home. However, the higher than expected death rates of certain age classes (calves and adult males) and the overall poor body condition of the translocated elephants indicates that elephants are nonetheless sensitive to translocation and that we should considered this when choosing elephants and release site locations in future translocations.

Finally, in Chapter Three, I explore the social behavior of the translocated elephants. Despite our extensive knowledge about the adaptive significance of sociality (Wilson 1975; Slobodchikoff 1988), very little work has thus far been conducted on the relationship between animals' social behavior and their familiarity with their habitat (Ward and Hart 2003; Griffiths 2003). I utilize the translocation to answer basic questions in animal behavior regarding animals' preferred group size in an unfamiliar environment. I also investigate with whom animals choose to interact when faced with a novel situation. I found that when the habitat was unfamiliar to the translocated elephants, they associated with more conspecifics than when the habitat became familiar to them. Furthermore, translocated elephants interacted more than expected with familiar conspecifics and less than expected with unfamiliar locals. However, the social segregation between the translocated and local populations dissolved over time. These findings suggest that there are added benefits to associating with conspecifics when placed in a novel setting and that elephants can integrate into an existing social setting. More broadly, I provide here important information about the relationship between social dynamics and habitat familiarity, a topic that has received very little attention in the study of animal behavior.

Overall, my work brings together applied and basic science to provide recommendations for practitioners based on animal behavior research, and to enhance our knowledge of basic animal behavior through examining management actions.

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Chapter 1

Exploration of a novel environment by translocated African elephants (*Loxodonta africana*)

Abstract

When choosing where to live in a novel environment an animal explores its new surroundings. Understanding the causes for variation in exploration behavior is important, especially when targeting individuals for conservation wildlife management actions such as reintroductions and translocations. In this study I explored the settlement process of translocated African elephants (*Loxodonta africana*) in a novel environment. I monitored the behavior and movement patterns of 12 radio collared African elephants for a year post-translocation. The extent of exploration behavior was negatively correlated with distance from observer and distance from roads. No relationship was found between final distance of elephants from release site and the amount of exploration exhibited. Furthermore, I documented the first account of African elephants homing back to their natal habitat. More males than expected left the release site, but females with calves also homed back to their natal habitat, demonstrating that homing is not confined to one sex or age. The work presented here suggests that both the exploration process and the final settlement distance from release site or natal nest should be addressed when studying animals in a novel environment, and not only one or the other. Furthermore, I suggest that explaining individual variation in spatial activity by linking it with other biological traits, which can be easily evaluated in the field, can provide useful management recommendations and interesting biological insights.

Introduction

Many species encounter, and must effectively cope with novel environments both naturally and due to human activities. For example, individuals of dispersing species search for, explore, and settle in novel habitats at certain life stages (Stenseth and Lidicker 1992; Stamps 2001) and migrating animals locate novel habitats periodically (Mettke-Hofmann and Gwinner 2004). Increasing human activities around the world expose many more animals to novel environments due to habitat loss (Sutherland and Dolman 1994) and fragmentation (Ewers and Didham 2006). Furthermore, wildlife management actions, such as reintroductions and translocations, expose animals to places they have never before encountered (Griffith et al. 1989; Sarrazin and Barbault 1996; Fischer and Lindenmayer 2000; Stamps and Swaisgood 2007).

While choosing where to live in a novel habitat, animals explore their new environment. The distance traveled during exploration and the time spent exploring entail both costs due to predation (Isbell et al. 1990, 1993; Larsen and Boutin 1994; Letty et al. 2002; Yoder et al. 2004), or exhaustion (Baker and Rao 2004; Stamps et al. 2005) and potential benefits such as gaining information about the new environment (Clark and Mangel 1984; Eliassen et al. 2007). Juvenile mammals often explore the surrounding habitat before dispersing from their natal home range (Wiggett et al. 1989; Harrison et al. 1991; Vangen et al. 2001; Selonen and Hanski 2006) and few studies of translocated animals have reported and quantified exploration behavior upon release at the new habitat (Ostro et al. 1999; Moehrenschlager and Macdonald 2003).

However, despite the costs of exploration (Moehrenschlager and Macdonald 2003; Baker and Rao 2004) and benefits of movement in a new habitat (Banks et al. 2002), many studies of translocated animals often overlook the exploration process and report only the final distance from the release site (Musil et al. 1993; Clarke and Schedvin 1997; Van Vuren et al. 1997; Armstrong et al. 1999; Cowan 2001). Final settlement location and its distance from the natal nest or release site can affect survival and fitness (Byrom and Krebs 1999; Hansson et al. 2004) but it does not always correspond to the amount of exploration exhibited (Moehrenschlager and Macdonald 2003; Tweed et al. 2003, Selonen and Hanski 2006). Thus, the potential consequences of exploration might not be reflected in the final distance from the release site or from the natal nest, and both distance and exploration should be addressed when studying the spatial aspects of behavior in a new environment.

Habitat exploration may vary between individuals within a species (Verbeek et al. 1994; Crook 2004; Doerr and Doerr 2005; Selonen and Hanski 2006), and can lead to variation in individual survival rates and fitness (Dingemanse et al. 2004). Linking exploration with other biological variables such as age (Mikheev and Andreev 1993), social setting (Stoewe et al. 2006), social dominance (Sunnucks 1998), life experience (Harris and Knowlton 2001), and boldness (Fraser et al. 2001) may provide useful proxies for predicting individual variation in exploration, and thus for predicting potential variation in survival.

To predict post-translocation variation in behavior it is important to choose biological variables that can be easily measured pre-translocation such as age, group size, and certain behavioral traits (Bremner-Harrison et al. 2004; Watters and Meehan 2007). Many translocations target animals living in proximity with humans, to solve human-wildlife conflict (Clarke and Schedvin 1997; Mosillo et al. 1999; Wambwa et al. 2001; Sullivan et al. 2004). Therefore, behavioral responses to human activities should be straightforward data to obtain pre-translocation. Distance to stationary experimenters and latency to approach them, also referred to as the ‘human approach test’, are used in farm animals to measure fear from humans (Hemsworth et al. 1989; Hemsworth et al. 1996; Breuer et al. 2000); and distance from roads is used as a measure of human activity avoidance (Theuerkauf et al. 2003; Whittington et al. 2005; Sawyer et al. 2007). These two behavioral measures can be easily assigned to individuals pre-translocation and therefore might prove useful if a relation between them and individual variation in exploration post-release is found.

This study describes the reaction to and exploration of a novel environment by African elephants (*Loxodonta africana*), an endangered species that is often translocated in wildlife management actions to solve human-elephant conflict (Muir 2000; Wambwa et al. 2001, Dublin and Niskanen 2003). The African elephants in this study were translocated from the coast of Kenya to Tsavo East National Park, a distance of 160 km. I examined the individual variation in distance from release site and in exploration patterns exhibited by the elephants in the novel environment and studied the relationship between exploration and biological variables such as age, group size, distance from observer, and distance from roads.

Methods

Translocation and study site

During September 2005, 150 African elephants were translocated from Shimba Hills National Reserve and Mwaluganje Elephant Sanctuary on the coast of Kenya (4°S to 4.3°S and 39.5°E to 39.3°E) to Tsavo East National Park (2.00°S to 3.70°S and 38.13°E to 39.30°E), a distance of 160 km (figure 1.1). This translocation was part of the Kenya Wildlife Service (KWS) elephant management program's effort to decrease and possibly resolve human-elephant conflict in the vicinity of Shimba Hills. The translocation was carried out by KWS and was funded by the Kenya Government. Elephant groups of fewer than 12 individuals were targeted for the translocation and were transported as an intact unit. Adult males were targeted based on their location and accessibility by road during the translocation and were moved in pairs. Translocating the 150 elephants took 32 days during which 20 groups (average group size 6.8 elephants) and 20 adult males were moved.

The release site, Tsavo East, differs greatly from the source site, Shimba Hills, in its climate, vegetation, size, and elephant density. Tsavo East is semi arid with an average annual rainfall ranging from 300mm to 700mm, while Shimba Hills is part of the coastal plateau with an average annual rainfall of 1500 mm and a humid equatorial climate. During the rains, vegetation growth in Tsavo East is spatially heterogeneous and unpredictable, in contrast to the spatially homogeneous and reliable vegetation growth in Shimba Hills. Tsavo East is the largest national park in Kenya (13,950 km^2) and along with the adjacent Tsavo West National Park forms the largest protected area in the country (20,812 km^2) whereas the source site, Shimba Hills is a small (250 km^2) reserve surrounded by human settlements. The two Tsavo National Parks (East and West) are home to the largest elephant population in Kenya (approximately 9,000 individuals (Blanc et al. 2007)) while Shimba Hills contains a small elephant population (approximately 600 individuals (Blanc et al. 2007)). The difference between the release and the source sites in area and in elephant numbers leads to a difference in the elephant population density: elephant density in Tsavo is 0.43 elephant per km^2 while elephant density in Shimba Hills is 2.4 elephants per km^2. These ecological differences between the release site and source site provide a unique opportunity to study the behavior of elephants in a novel environment (the release site) they have never before encountered.

Data collection

During the translocation all elephants were individually marked for post-translocation monitoring. All 150 elephants were tagged with yellow zip ties on their tails and painted with a unique white number on their backs for individual identification, survival analysis, and general post-translocation monitoring. The age of each translocated elephant was estimated, according to body measurements (back length and shoulder height) taken during the translocation and observations later in the field, based on Moss (1996). Of the translocated elephants, 12 adults (3 males and 9 females) moved on different days, were fitted with GPS/VHF elephant collars (Sirtrack, New Zealand) to enable detailed post-release tracking of movement patterns.

Post-translocation monitoring was conducted for 380 days after the release of the first group, providing at least a year of data for all translocated elephants. Collared elephants were tracked from the air and ground by locating the VHF signal of their radio collar using a TR-4 Tracking receiver (Telonics, USA). On the ground, a three element hand-held folding Yagi antenna (Sirtrack, New Zealand) was used to detect the signals from the elephant collars. A compass was used to determine the bearing towards the signal and a Geko 201 GPS unit (Garmin Ltd., USA) was used to record the location from which the bearing was taken. The computer program Locate II (Nams 2000) was later used to determine the location of the collared elephants through triangulation. Tracking from the air was conducted using a light Super Cub aircraft fitted with wing-mounted antennae. Signal directionality was determined using a TAC-2-RLB Antenna Control Unit (Telonics, USA). The elephants were located and identified from the air and their location was recorded using a Geko 201 GPS unit (Garmin Ltd., USA). Each collared elephant was sought at least 2-3 times a week, from air and ground, and located at least once a month.

During ground and aerial surveys, the location and identity of every translocated elephant seen was recorded. Individual's identities were recorded only when a positive identification was obtained based on collar frequency, painted number, or ear patterns. This provided data on the status of all translocated elephants, and not only collared individuals. Analysis of exploration patterns, however, was based only on data from collared individuals, due to the higher temporal resolution of collared individual sightings. Attempts to include sightings of uncollared individuals in the exploration analysis showed a systematic bias resulting from the small sighting number for these elephants.

Despite the fact that elephants are social animals with strong social bonds among group members (Moss and Poole 1983), the number of individuals associating with the collared elephants varied throughout the study due to the fission-fusion characteristics of elephant societies (Moss and Poole 1983; Wittemyer et al. 2005; see also Chapter 3). Therefore, to determine whether group size had any effect on the behavior of the elephants post-translocation, an average group size was calculated for each collared elephant. Membership in a group was defined based on behavioral coordination and spatial proximity. For example, elephants engaged in a similar task e.g., walking, and within approximately 100 m or less of each other, were considered to be members of the same group.

Minimal distance between elephants and a stationary observer was roughly estimated for each ground observation of the collared elephants, in a similar manner to obtaining minimal distance to the observer in a 'human approach test' conducted in farm animals (Hemsworth et al. 1996). Minimal distance to observer was assigned only to actual sightings and did not include triangulation data for which the elephants were not actually sighted. When collared elephants were sighted during ground surveys, the observer stopped the vehicle and remained stationary while observing the elephants' behavior. Observations were carried out until the elephants could no longer be seen, a duration that allowed enough time for the elephants to sense the observer's presence. The minimal distance between a collared elephant and the stationary observer during the observation period was recorded as being either less than 0.1 km, 0.1 km to 1 km, or grater than 1 km. The average minimal distance to observer across sightings was calculated for each collared elephant, and statistical analysis was conducted on the log of this average.

Data analysis

Last distance from the release site and distance from roads were calculated based on the locations obtained for the collared individuals. Last distance from release site was calculated as the straight Euclidian distance between the release site and the location where the collared elephant was last seen. Distance from roads was calculated for each collared elephant location based on GIS data obtained from the Tsavo East research station and the use of ArcView 3.2 (ESRI, USA).

A Moving Weighted Centroid (MWC) analysis was developed to accurately describe exploration patterns, taking into account the patchy manner in which elephants use their habitat.

Elephants exhibit a heterogeneous usage of their habitat by moving great distances rapidly between areas of high use, also referred to as streaking (Douglas-Hamilton et al. 2005). This heterogeneous habitat use is equivalent to nomadism described and reviewed by Sinclair (1984) and is similar to movement patterns of other mammals (Sheppard et al. 2006). In the MWC analysis I calculated the distance of each collared elephant location (focal location) to the centroid of its locations from the previous 30 days. The centroid was calculated as a spatio-temporal weighted average:

$$X = \frac{\sum_{i,t_i \le 30} x_i \times \frac{1}{t_i}}{\sum_{i,t_i \le 30} \frac{1}{t_i}}$$

$$Y = \frac{\sum_{i,t_i \le 30} y_i \times \frac{1}{t_i}}{\sum_{i,t_i \le 30} \frac{1}{t_i}}$$

Where X and Y are the x, y coordinates of the centroid; x_i and y_i are the x, y coordinates of a sighting (i) within the 30 days preceding the focal location; and t_i is the number of days separating a sighting (i) from the focal location.

Weighing each location inversely proportional to the number of days separating it from the focal location assigned earlier locations a lower impact on the location of the centroid. Since the centroid for each new location was based on data from the 30 days preceding the focal location, the centroid moved over time, and overall effectively created a moving average of the general movement patterns for each elephant.

The MWC is an extension of using a fixed time window, which creates discrete activity centers, as described in Waterman (1986). In expansion of the discrete activity centers, the MWC analysis creates a continuous activity center by employing principles from smoothing techniques, which are often used when analyzing animal movements, such as moving windows (Pace 2001), moving average (MA), and moving weighted average (MWA) (for a review of smoothing techniques see (Hen et al. 2004)). However, in contrast to such smoothing techniques, whose goal is to average the movement pattern, in this study the deviation from the average smoothed movement was of interest as an exploration measure. Calculating the distance (d) of each observation from the MWC provided information regarding the amount of localized movements each elephant exhibited during its exploration of the novel environment. The statistic used to describe the exploration value for each elephant was the median of d for all observations over a course of a year. These calculations were conducted in Matlab (MathWorks Inc., USA).

Statistical Analysis

To determine whether the number of translocated elephants that left the release site, Tsavo (East and West) National Parks, differed from expected values based on the proportion of males to females in the translocated elephant population, a Chi Square test was used. Expected number of elephants leaving the release site was calculated based on the number of adult males (N=15) and the number of females, juveniles, and calves (N=94) within the population of translocated elephants whose fate was known (N=109) and the total number of elephants that left the release site (N=8) (see Chapter 2 for more details on the fates of the translocated elephants). Variability among elephants in last distance from release site and in exploration was expressed as a coefficient of variation (C_v).

To study the relationship between exploration and other biological variables, a linear regression was used for assessing the relationship between age and exploration and a Pearson's correlation coefficient was used to associate exploration with all other variables (group size, minimal distance to observer, and distance to roads). Correction for multiple testing was conducted using the False Discovery Rate (FDR) method (Benjamini and Hochberg 1995). Consequently, statistical significance was set at p-values less than 0.025 for testing the relationship between exploration and other biological variables. All statistical analysis was conducted in Matlab (MathWorks Inc., USA) using the statistical toolbox.

Results

Leaving Tsavo East and West National Parks

Eight of the 150 translocated elephants left the release site, Tsavo (East and West) National Parks, and either returned to Shimba Hills or ended up elsewhere on the coast. Of these eight elephants, two males, one collared and one uncollared, were found on the coast, 170 km east of the release site, 13 and 31 days after release. A collared female and her calf were found in Shimba Hills 12 days after release. Two other males, one collared and one uncollared, were sighted in Shimba Hills 54 and 171 days after release. Another collared female and her calf were found in Shimba Hills 165 days after release. This female and her calf were seen in Tsavo East six weeks earlier, when the rains began, indicating that they must have homed back to the source site during those six weeks, at least 123 days after their release, and not immediately upon release. This last observation implies that ecological factors, such as rain, might play a role in the timing of homing events.

Two travel paths of collared elephants that left the release site were closely monitored, the path of the male that took 13 days to reach the coast and the path of the female and her calf that took 12 days to reach Shimba Hills (figure 1.1). Monitoring these paths revealed direct movements with hardly any deviations from a straight line connecting the release site and the final location. Despite the fact that exploration values, as calculated for other collared individuals later, could not be obtained for these two individuals due to their short travel duration, a qualitative difference between their movement patterns and those of elephants that remained in Tsavo East can be seen in figure 1.1.

Both females that homed back to Shimba Hills left their social group behind. Some of the remaining group members were seen in Tsavo East more than half a year after the homing females left. Finally, more males and fewer females with calves than expected, left the national park, to which they were released, and either homed back to the source site or elsewhere on the coast (chi square, $P<0.01$) (figure 1.2).

Individual variation in spatial use of elephants that remained near the release site:

Of the 12 collared elephants, only seven remained in the Tsavo (East and West) National Parks (four collared individuals rejected the release site and were discussed above, and one died four days after release). An average of approximately 80 locations (range: 19-125) through triangulation and sightings from ground and air were obtained for each of the seven remaining collared elephants. Last distance from release site varied extensively between the remaining seven collared elephants ($C_v = 77\%$, range: 9.3-102.5 km). Furthermore, exploration values, as estimated by the median distance from the MWC, also varied greatly among these elephants ($C_v = 62\%$, range: 2.2-11.6 km). Each elephant had a different exploration pattern in regard to its MWC: some elephants ranged far from their MWC whereas others remained close to their MWC at all times (see figure 1.3 for a comparison between exploration patterns of two collared elephants).

Interestingly, no relationship was found between exploration and final distance from release site (Pearson correlation, r = 0.02, p = 0.97, N=7) (figure 1.4), indicating that elephants with high exploration values did not necessarily settle far from the release site, and vice versa.

Relationship between exploration and other variables

Minimal distance to observer and distance to roads correlated strongly with exploration. The log of the average minimal distance to observer negatively correlated with the exploration measure (Pearson correlation, r = -0.89; p=0.02, N=6) (figure 1.5). Average distance to roads also negatively correlated with the exploration patterns observed (Pearson correlation, r =-0.86, p = 0.01, N=7). Correlations of exploration with distance to observer and with distance to roads achieved statistical significance after correcting for multiple testing (m=4 tests). Exploration patterns did not significantly correlate with age (r= 0.02, p=0.96, N=7) or with average group size (Pearson correlation, r = -0.54; p = 0.27, N=6).

Discussion

The translocated elephants' reaction to the novel environment varied greatly. Some elephants left the release site and homed back to the source site, while others remained in the national park to which they were released. Furthermore, among the elephants that remained in the national park, great individual variation was found in their exploration of the new habitat.

Leaving the release site and homing

Never before has homing been documented in African elephants (but see Muir (2000) for an account of males who went from Tsavo East to the coast, but not to their natal habitat; and Lahiri-Choudhury (1993) for homing in translocated Asian elephants). Still, homing is often observed in other translocated animals (Clarke and Schedvin 1997; van Vuren et al. 1997; Cowen 2001; Bowman et al. 2002; Sullivan et al. 2004). Elephants are capable of traveling great distances (Viljoen 1989; Thouless 1995) and may return to locations they have not visited in many years (Foley 2002). In this study, however, elephants were translocated in conditions which did not allow visual, olfactory, and acoustic cues during transport, but nonetheless accurately returned to their source site. This raises questions regarding the mechanisms underlying elephant homing abilities which cannot be answered by this study. The fact that two males reached the coast, but not the source site itself, may suggest use of olfactory cues brought by coastal winds, or alternatively, use of river directionality.

Homing of the translocated elephants was not confined to one sex or age. Individual variation in travel distance from release site can sometimes be explained by age and sex (Tuberville et al. 2005) but not always (van Vuren et al. 1997; Cowen 2001). In the study presented here, more males than expected left the release site, possibly due to males being the dispersing sex in elephants and being accustomed to traversing great distances when looking for mates (Moss and Poole 1983). However, females and calves were also found to leave the release site and home back to the source site, suggesting that all elephants, including very young calves, are capable of traversing substantial distances over a short time period.

Elephant homing events were not limited to a certain time after release, despite reports of homing events in other species occurring immediately after release (Belisle et al. 2001; Sullivan et al. 2004). Some elephants indeed returned to the source site as soon as they were released, while others waited until the rains began before homing. Seasonal variation in movement patterns was previously observed in translocated fox squirrels (Bendel and Terres 1994) and was explained by food abundance differences between spring and fall. Thus, elephants that homed during the wet season might have been inhibited from doing so earlier by lack of sufficient forage which increases substantially following the rains. Such late homing events might be overlooked when translocated animals are monitored for a short period of time post-translocation. Therefore, monitoring duration spanning all seasons can be crucial in heterogeneous environments (such as the release site in this study) where seasonal differences are drastic and may induce extensive, unexpected movements.

Finally, homing females left their social groups behind, taking with them only their youngest calf. Homing events of entire social groups were not documented here. This observation may provide insights regarding the dynamics of group decision making, about which very little is known (Wilson 2000; Byrne 2000). Synchronization of group activities, such as deciding when and where to move, can involve significant conflicts (Conradt and Roper 2005). A recent model (Conradt and Roper 2003) showed that democratic decisions are beneficial to all group members unless the leader is very experienced and should then be followed as a despot. However, in a novel environment all group members are equally unfamiliar with the new habitat. The fact that homing females left their groups suggests that the costs of reaching a group consensus and attaining synchronized group movement post-translocation might have outweighed the benefits of remaining in a group (Conradt and Roper 2003, 2005). However, further research is needed to determine the actual underlying causes of group fissions in a novel environment.

Variation in exploration of the novel environment

When considering the behavior of individuals that remained in proximity to the release site, great variation was found in the levels to which they explored their new environment. Individual variation in exploration patterns has been found in other translocation studies (Moehrenschlager and Macdonald 2003; Crook 2004). To examine the variation in exploration of a novel environment in this study I developed the Moving Weighted Centroid analysis. The MWC analysis encompassed a nested model of spatial movement separating small scale local movements from the general overall movement patterns of the animal. While the overall large scale movements dictated the end location of the animal, the small scale movements around the centroid described the exploration characteristic of the animal. A similar fractal-like nested movement pattern to that obtained when using MWC analysis, was also described in treecreepers when using different analysis techniques (Doerr and Doerr 2004). Thus, MWC is an exploration measure relevant to the study species that can provide a fine-grained detailed description of movements which is comparable to techniques used in other studies.

A negative significant relationship was found between exploration levels and the distance elephants allowed between themselves and human activities in this study. Explaining individual variation in exploration of a novel environment can have conservation and wildlife management implications when targeting individuals for translocations and reintroductions. For example, juvenile swift foxes were found to explore less and to have higher survival rates than adults, leading to a recommendation of targeting juveniles for future translocations (Moehrenschlager and Macdonald 2003). Furthermore, behavioral indicators that can be easily evaluated pre-translocation can prove to be useful for predicting post-translocation behavior and even survival (Watters and Meehan 2007). For example, reaction to novel objects prior to release was found to negatively correlate with survival and positively correlate with movement distance from release site in swift foxes (Bremner-Harrison et al. 2004). In the study presented here, exploration was found to tightly correlate with behavioral variables relating to the animals’ reaction to human activities: minimal distance to observer and distance from roads. These two variables can be easily measured and assessed in the field both pre- and post-translocation, thus providing a surrogate for estimating exploration of uncollared elephants and acting as indicators for post-release exploration levels when targeting individuals for translocation.

Finally, in this study, no relationship was found between exploration and final distance from release site. Individuals found at a similar end distance from the release site did not exhibit similar exploration behavior and therefore might not have incurred similar costs, or gained similar benefits (ecological information) during the settlement process. Selonen and Hanski (2006) found that juvenile flying squirrels differ in the amount of pre-dispersal exploration they exhibit. Some juvenile flying squirrels explore the environment before dispersal and therefore settle in a familiar location, whereas others do not explore the environment before dispersal and therefore settle at a similar distance from their natal nest, but in an unfamiliar location. Furthermore, long-distance dispersers often exhibit low levels of exploration (Byrom and Krebs 1999; Selonen and Hanski 2006), similar to the direct movements, seen in the homing elephants or those that reached the coast (figure 1.1). Thus, examining only end distance from the release site in translocated animals, or from the natal nest in dispersers, might overlook variation in survival consequences originating from variation in exploration.

Overall, the results presented here suggest that the final distance from release site and exploration of a novel environment can vary greatly within a population. The lack of relationship found between these two spatial measures in this study suggests that both should be considered when studying animals in a novel environment, and not only one or the other. Finally, being able to explain individual variation in exploration or in final distance from the release site by linking them with other biological traits, which can be easily evaluated, can both augment wildlife management decisions, and provide interesting insights regarding animal behavior in general.

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Figure legends

Figure 1.1: Map of field site and movement paths of three collared elephants.
Inset indicates location of field site within Kenya; light gray polygons represent the protected areas Tsavo East National Park, Tsavo West National Park, Shimba Hills National Reserve, and Mwaluganji Elephant Sanctuary (MES); dark gray lines denote permanent rivers; release site is marked with a star; the travel rout of a collared male who reached the coast within 13 days of release is indicated by a dashed black line; the travel rout of a collared female and her calf who reached Shimba Hills within 12 days of release is indicated by a dotted black line; and the travel path of a collared female who remained in Tsavo East, based on locations obtained throughout the year of the study, is presented for comparison by a thin solid black line.

Figure 1.2: Observed and expected number of elephants that left the release site. Black bars indicate the observed number of elephants who left the release site. Open bars are expected values calculated based on the ratio of adult males to females and calves in the population of translocated elephants whose fate is known, and the total observed numbers of elephants that left the release site. Differences between observed and expected values are statistically significant: Chi square, $P<0.01$.

Figure 1.3: Distance from MWC (d) over time for two translocated elephants. For each sighting, its distance (d) from the spatial centroid of the preceding 30 days is indicated in km on the y axis. Sightings from 6 months post-translocation are shown (time indicated on the x axis). Open circles are sightings of a collared female with high exploration values. Closed circles are sightings of a different collared female with low exploration values.

Figure 1.4: Exploration vs. last distance from release site. Exploration is the median distance from the MWC for each elephant (km). Last distance from release site (RS) is the Euclidian distance between the release site and the location where the elephant was last seen (km). No correlation was found between these two variables (Pearson correlation, $r = 0.02$, $p = 0.97$).

Figure 1.5: Exploration vs. minimal distance from observer. Exploration is the median distance from the MWC for each elephant (km). Distance from observer is the average minimal distance

from observer for all actual sightings from the ground of each elephant (km) and is plotted on a Log scale. A strong negative correlation was found between minimal distance to observer and exploration (Pearson correlation, r = -0.89; p=0.02).

Figure 1.1

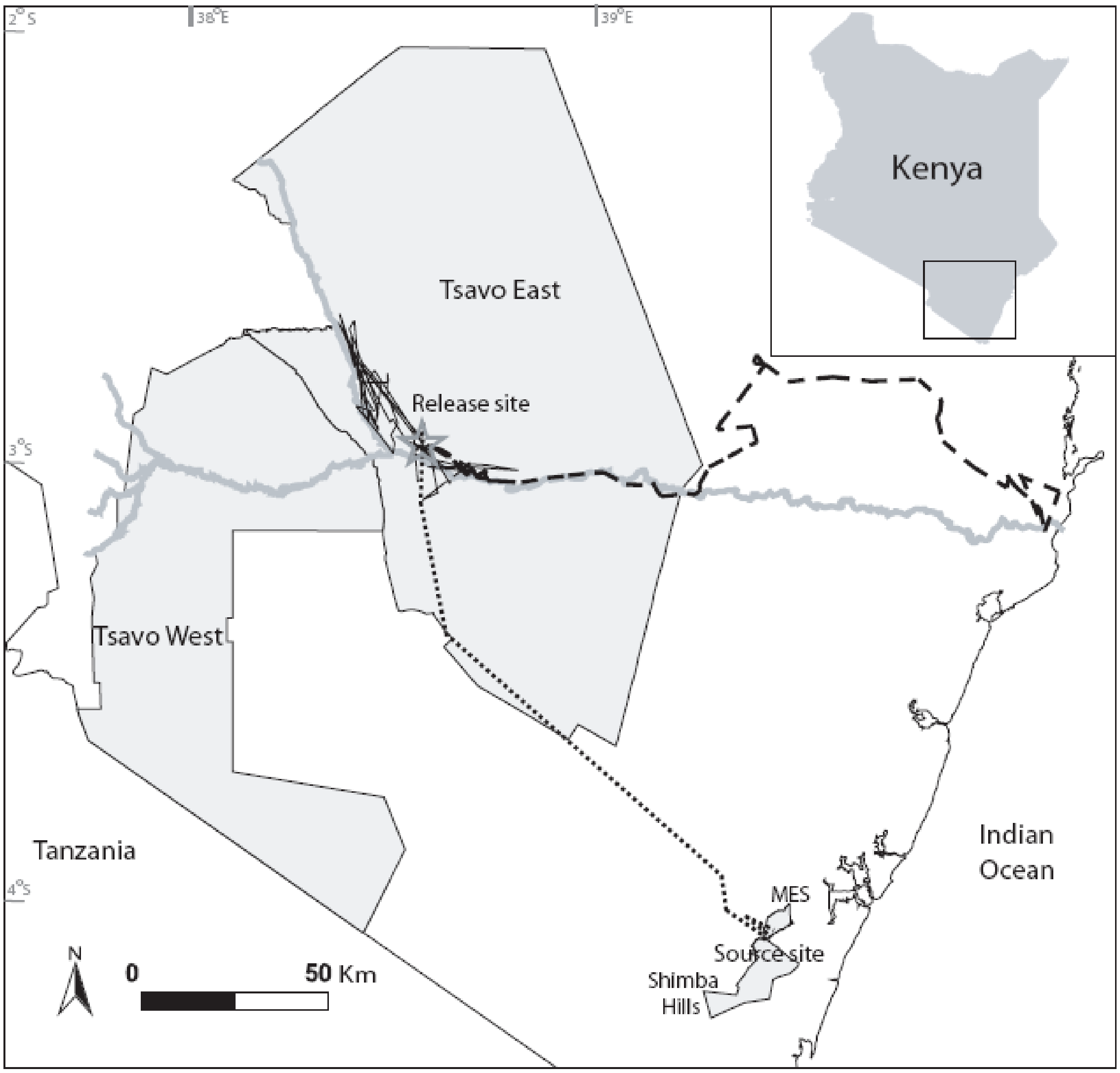
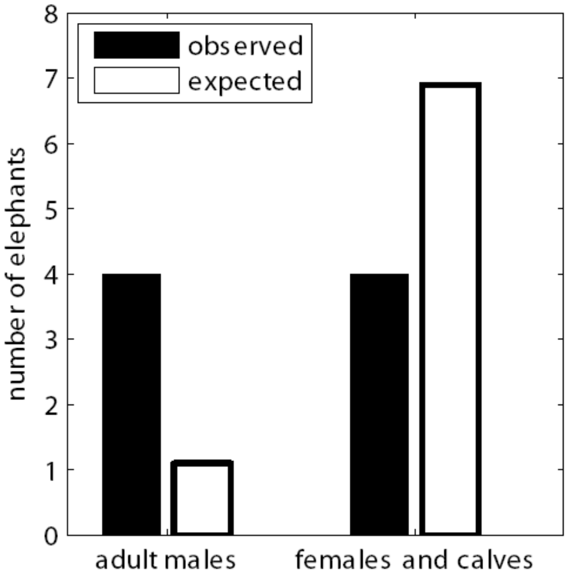


Figure 1.2



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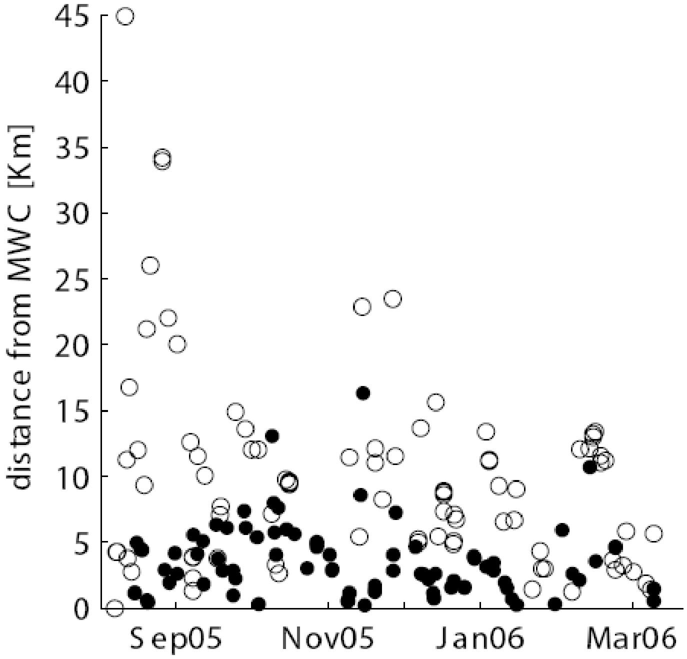


Figure 1.4

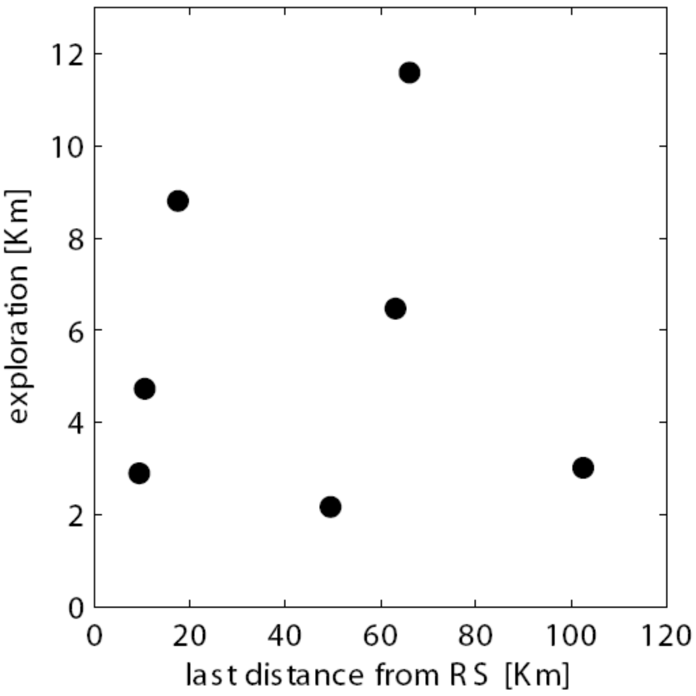
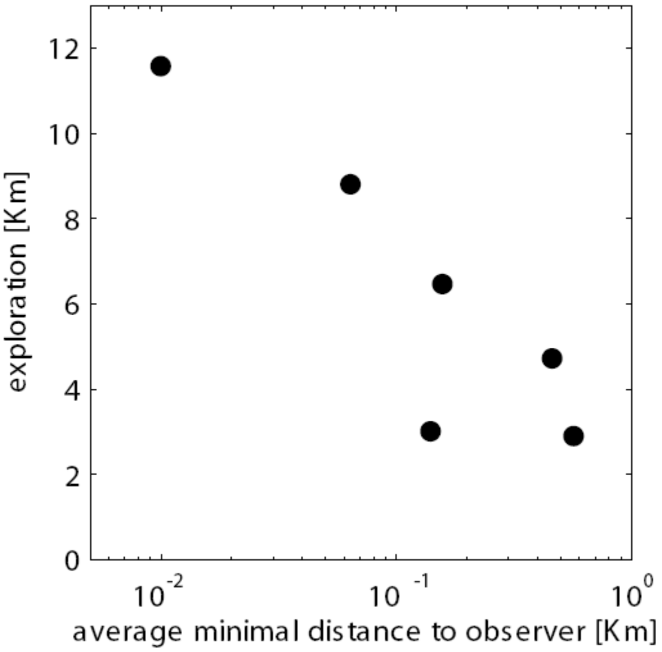


Figure 1.5



Chapter 2

The behavioral and physiological convergence of translocated African elephants with a local resident population

Abstract

Evaluating translocation outcomes is important for improving wildlife management and conservation actions. Often, when quick decisions need to be made and long-lived animals with slow reproduction rates are being translocated, traditional assessment methods such as long-term survival and reproductive success cannot be used for assessing translocation outcomes. Thus, alternative, seldom used, measures such as comparing the behavior and physiology of translocated animals to those of local residents should be employed to assess the acclimation of the translocated animals to their new home. Here I monitored the survival, physiology, and behavior of translocated African elephants (*Loxodonta africana*) and compared these measures to those of the local resident population at the release site. Adult translocated elephants' death rates were higher than those of the local population. Furthermore, the mortality rate of translocated adult males and calves was greater than expected based on their proportion in the translocated elephant population. No difference was found in the stress hormone levels between the two populations, but the body condition of the translocated elephants was significantly poorer than that of the local population throughout the study period. The behavior of the translocated elephants converged with that of the local population over time. Finally, translocated elephants spent more time in habitat that was similar to their source site (hills and permanent rivers) than did the local population. These findings provide an evaluation of recent conservation actions, recommendations for future wildlife management actions, and more broadly introduces and explore the use of new assessment techniques for evaluating translocations.

Introduction

Relocating animals from one location to another is a common management tool used for different conservation purposes. For example, animals that have become either globally or locally extinct in the wild are reintroduced to their historical range (Perelberg et al. 2003; Richards and Short 2003; Brightsmith et al. 2005; Bar-David et al. 2005; Seddon et al. 2007). Animals are also translocated for rescue purposes (e.g., before intentional habitat destruction: Ostro et al. (1999); Richard-Hansen et al. (2000); Edgar et al. (2005)), and for solving human-wildlife conflicts (Jones and Nealson 2003; Wambwa et al. 2001). However, only 44% of translocations of endangered, threatened, or sensitive species are successful (Griffith et al. 1989) and most translocations aimed at solving human-animal conflicts fail (Fischer and Lindenmayer 2000). These low success rates reveal the importance of monitoring animals post-release to determine the factors leading to translocation success or failure.

Ultimately, translocations and reintroductions are considered successful if they result in self-sustaining populations (Fischer and Lindenmayer 2000). However, it may take a long time to evaluate whether a population is viable, especially when dealing with long-lived animals. Therefore, other parameters are often used to assess the ability of released animals to become established in their new home. Mortality and reproductive success are directly related to population viability and therefore are often reported (Warren et al. 1996; Richard-Hansen et al. 2000; Clarke et al. 2003). Certain behaviors can also provide suitable measures for determining the ability of animals to become established at the release site. For example, whether released animals are able to forage efficiently can be used to infer their chances of long-term survival in the new location (Bright and Morris 1994) and the movement patterns and habitat choice of released animals determine whether they will remain at the release site or leave it (Clarke and Schedvin 1997; van Vuren et al. 1997; Cowan 2001; Moehrenschlager and Macdonald 2003; Sullivan et al. 2004; Stamps and Swaisgood 2007).

In addition to demographic and behavioral data, physiological measures such as body condition and stress hormones may also provide suitable indicators for translocation success and can supply mechanistic explanations for the animals' response to the novel environment (Wikelski and Cooke 2006), yet they are seldom used for translocation assessment. Components of body condition such as body mass (Molony et al. 2006; Field et al. 2007) or pregnancy rate (Clifford et al. 2007), are indicators of an animal's energy reserves and reproductive ability and are therefore directly linked to survival and to the ability of a population to become established in its new home, thus providing a convenient measure for assessing the outcome of a translocation. Stress measures, such as steroid metabolites, can inform managers about the welfare of the translocated animals and about their ability to survive at the release site (see review in Teixeira et al. (2007)). For example, an increase in glucocorticoids (GC) immediately after release can induce a flight response when encountering unfamiliar objects, thus potentially reducing predation incidents (Teixeira et al. 2007). However, abrupt elevation of GC during the translocation procedure itself may be a sign of reduced animal welfare (Waas et al. 1999) and prolonged exposure to high GC levels can inflict severe damage to animals' memory and immune system, leading to reduced survival (Teixeira et al. 2007).

Obtaining biological measures for assessing the outcome of translocations with no baseline for comparison may have little value. One option is to compare post-translocation measures with pre-translocation measures. It is not always possible to obtain pre-translocation data, however, and when animals are moved to a place that is very different from the source site, their original pre-translocation behavior may no longer be relevant in the new location (Warren et al. 1996). The local resident population at the release site is presumably well acclimated to the release site and therefore can provide a good baseline for comparison, for example, when comparing survival rates (Molony et al. 2006; Frair et al. 2007), habitat choice (Ostro et al. 2000), movement patterns (Molony et al. 2006), and range use (Ostro et al. 1999). Although comparing translocated animals to a local population may not be feasible when translocations are used for restocking vacant habitat, often a local population is present, but is not taken advantage of as a baseline for comparison (e.g., Clarke and Schedvin (1997); Tweed et al. (2003); and Goossens et al. (2005)).

Assessing translocations using behavioral and physiological measures and comparing them with a local resident population at the release site is especially useful when dealing with long-lived animals whose survival and reproductive success may take years to assess, and when management decisions must be reached rapidly. African elephants (*Loxodonta africana*) are long-lived animals (up to 65 years) with a very slow reproductive rate (4.5 years interbirth interval) (Moss 2001) for which such assessments would be particularly helpful.

African elephants are placed in the paradoxical position of being simultaneously a vulnerable species which needs to be conserved (IUCN 2004), and a pest due to human-elephant conflict resulting from human encroachment onto elephant habitat (Hoare 1999; Hoare 2000; Lee and Graham 2006). Many solutions to this problem have been used, some more successful than others. For example, deterrents such as electric fences (O'Connell-Rodwell et al. 2000) and the plant *Capsicum oleoresin* (hot chili pepper) (Osborn 2002) are useful where elephants have alternative habitats. However, most cases of human-elephant conflict occur in highly populated areas where no alternative habitat for the elephants is available (Balfour et al. 2007). In such situations, solutions include culling (van Aarde et al. 1999), birth control (Pimm and van Aarde 2001), and translocating elephants to new locations (Muir 2000; Wambwa et al. 2001; Dublin and Niskanen 2003). Of these potential solutions, translocation is the most humane and sensitive to the elephants' vulnerable conservation status. However, very little post-translocation research has been conducted to determine whether these massive management actions are successful (for reports on the outcome of male elephant translocations see Muir 2000; Garai and Carr 2001; and Slotow and van Dyk 2001).

Here, I compared the survival, behavior, and physical condition of translocated elephants to those of the local elephant population at the release site for a year post-release. Mortality immediately after release provided information about the short-term consequences of the translocation operation itself. Behavior, habitat use, and physical measures, such as body condition and stress hormone levels, were compared between the translocated individuals and the local elephants. This comparison provided an account of the translocated elephants' acclimation process to their new home and was used to assess the outcomes of the translocation. Movement patterns and social interactions of these translocated elephants in their new habitat are reported elsewhere (Chapters 1 and 3). This study is the first to utilize both behavioral and physiological measures for assessing the outcome of a translocation of a long-lived animal. In addition, the ability to capitalize on the presence of a resident elephant population at the release site to better assess the translocation outcome is unique and seldom found in studies of translocated animals. Thus, I present here novel assessment methods that I believe will be vital for many future studies on the outcomes of conservation actions.

Methods

Translocation and study site

During September 2005, 150 African elephants were translocated from Shimba Hills National Reserve and Mwaluganje Elephant Sanctuary on the coast of Kenya (4°S to 4.3°S and 39.5°E to 39.3°E) to Tsavo East National Park (2.00°S to 3.70°S and 38.13°E to 39.30°E), a distance of 160 km. This translocation was part of the Kenya Wildlife Service (KWS) elephant management program's effort to decrease and possibly resolve human-elephant conflict in the vicinity of Shimba Hills. The translocation was carried out by KWS and was funded by the Kenya Government. Elephant groups of fewer than 12 individuals were targeted for the translocation and were transported as an intact unit. Adult males were targeted based on their location and accessibility by road during the translocation and were moved in pairs. Translocating the 150 elephants took 32 days during which 20 groups comprised of adult females, juveniles, and calves (average group size 6.8 elephants) and 20 adult males were moved.

The release site, Tsavo East, differs greatly from the source site, Shimba Hills, in its climate, vegetation, size, and elephant density. Tsavo East is semi-arid with an average annual rainfall ranging from 300mm to 700mm, while Shimba Hills is part of the coastal plateau with an average annual rainfall of 1500 mm and a humid equatorial climate. Tsavo East is the largest national park in Kenya (13,950 km^2) and, along with the adjacent Tsavo West National Park, forms the largest protected area in the country (20,812 km^2) whereas the source site, Shimba Hills is a small (250 km^2) reserve surrounded by human settlements. The two Tsavo National Parks (East and West) are home to the largest elephant population in Kenya (approximately 9,000 individuals (Blanc et al., 2007)) while Shimba Hills contains a small elephant population (approximately 600 individuals (Blanc et al., 2007)). These differences between the release site and source site and the existence of a local resident elephant population at the release site provided a unique opportunity to compare the behavior and physiology of translocated elephants to a local population in a novel environment (the release site).

Data collection

During the translocation all elephants were individually marked for post-translocation monitoring. All 150 elephants were tagged with yellow zip ties on their tails, to distinguish them from the Tsavo elephant population, and were painted with a unique white number on their backs for individual identification, survival analysis, and general post-translocation monitoring. The age of each translocated elephant was estimated, according to body measurements (back length and shoulder height) taken during the translocation and observations later in the field, based on Moss (1996). Of the translocated elephants, 12 adults (three males and nine females) moved on different days were fitted with GPS/VHF elephant collars (Sirtrack, New Zealand) to enable detailed post-release tracking of movement patterns.

The locations of translocated and local Tsavo elephants were recorded for one year post-translocation. Road transects in Tsavo East were conducted using a vehicle 4-5 times a week, alternating between four different routes of similar length (50-70 km) on existing roads within Tsavo East National Park. All elephants sighted during the transects were noted. Furthermore, aerial surveys were conducted 2-3 times a week, to locate collared individuals in Tsavo East, Tsavo West, and the surrounding ranches. The location of all translocated and local Tsavo elephants seen during the aerial and ground surveys were recorded using a Geko 201 GPS unit (Garmin Ltd., USA). The locations of translocated collared elephants were also recorded through triangulation during ground surveys, using the computer program Locate II (Nams 2000) to calculate their exact locations.

Survival

Post-translocation monitoring and reports from various sources were used to determine the survival of the translocated elephants. Reports of dead elephants with tail tags and white numbers were verified and cause of death determined, when possible. Calves (age class 0-5) that were seen with their mothers initially after release, but were then missing when their mother was sighted again, were defined as ‘probably dead calves’. Since elephant calves suckle until the age of four and are highly dependent on their mothers, a female that is seen without her calf strongly suggests that the calf is dead (Moss 2001). The date during which a mother was first sighted without her calf was recorded as the death date for that calf.

I first determined whether deaths of translocated elephants were distributed among adult males, adult females, juveniles, and calves as expected based on their respective proportion in the population of translocated elephants whose fate is known, using a chi-square test. Next, I compared the death rates of the translocated elephants to those of the local Tsavo population using records of elephant deaths from the Tsavo East research station. Only adult translocated elephants that died after the translocation (and not during it) were used in this comparison because records of dead local elephants are based on elephant bodies found in and around the national park and bodies of calves are rarely found (no dead calves were recorded in the research station's database).

A binomial distribution was used to calculate the probability that a translocated elephant would die at the release site, based on the estimated death probability of the local Tsavo East elephants. The probability of death of a given Tsavo elephant was calculated as the proportion of dead local elephants reported during the year of this study (N=77) out of the estimated number of elephants in Tsavo East (N=6395), based on an aerial count conducted in 2005 (Omondi and Bitok 2005).

Body condition

To evaluate whether the physical state of translocated elephants differed from that of the local Tsavo elephants, the body condition of elephants sighted during ground surveys was recorded. The body condition index used was based on work by Wemmer et al. (2006) who developed a body condition index for Asian elephants. When elephants were clearly visible (not obstructed by vegetation), four body regions' conditions were assessed: head, shoulder blade (scapula), thoracic region (rib cage), and pelvic bone. Each body region was assigned a score between 0-2 based on the criteria described in table 1 (A,B,C, and F) in Wemmer et al. (2006) with zero being the least body mass observed in a certain body region and two being the greatest. Due to field conditions under which all body regions could not always be scored, an average score of all assessed regions was used as the body condition parameter for each elephant, and not the total of all region scores as in Wemmer et al. (2006). Only data for adult elephants were used here due to a significant effect of age class found during initial analysis of the data and because the body condition index was developed for adult elephants.

Females' mammary gland condition was also recorded when possible. Mammary glands were assigned to three categories (0-2) based on their fullness. A score of zero was assigned to flat mammary glands that looked no different from the thorax of a male, one was assigned to full but small mammary glands (hidden behind front legs when standing), and two was assigned to full and large mammary glands (not obstructed by front legs when standing).

Hormone collection and analysis

When possible, fecal samples were collected from both translocated and local Tsavo elephants, for stress hormone analysis. The entire dropping was thoroughly mixed and sampled as described in Foley et al. (2001). Approximately 50cc of the mixed sample were immersed in 96% ethanol for preservation and stored in polystyrene Falcon tubes at a temperature of -18°C. All samples were analyzed after being stored for more than one year to eliminate storage time effects on the fecal glucocorticoid levels described in Hunt and Wasser (2003). We used the Corticosterone Double Antibody I-125 RIA Kit (MP Biomedicals, OH, USA) to extract corticosterone metabolites from the fecal samples (see extraction details in Wasser et al. (2000) and Hunt and Wasser (2003)).

Behavior

To compare the time budget of the translocated elephants to that of the local Tsavo elephants, all elephants' behaviors were recorded when sighted during ground surveys. Three behavioral categories were defined: Foraging (any type of resource acquisition): feeding on bush or grass and drinking form a river or water hole; Walking: moving continuously across the landscape; Standing: resting while not foraging or walking, usually exhibited as a group of motionless elephants in a tight formation, often in the shade of a tree. To avoid pseudo-replication of the data caused by all members of a social group (elephants within 1-5 body distances from one another) performing the same behavior, the modal behavior for all group members, obtained through a scan sample of all group members when first sighted, was recorded and considered one behavioral record.

Habitat use

To examine whether translocated elephants and local Tsavo elephants differed in their habitat use, data on elephant locations from ground (direct sightings and triangulation) and aerial surveys were overlaid on GIS data obtained from the Tsavo East research station. The habitat in Tsavo East was categorized into four types based on vegetation cover, water source, and topography: bush, bushed grasslands, permanent rivers, and hills. Bush habitat was defined as habitat comprised of 20-40% shrub cover and less than 20% grass cover. Bushed grasslands (bush-grass) habitat was defined as areas with shrub cover of 2-20% and more than 20% grass cover. Permanent rivers (perm-river) habitat included all locations within 0.5 km of a permanent river (permanent rivers in Tsavo East include the Galana, Athi, and Tsavo Rivers). Although plant cover in the permanent river habitat was mostly bushed grassland, the area defined as permanent rivers was not included in the bushed grassland category to avoid double-counting sightings for more than one habitat. Hills habitat was defined based on topography and was mostly (99%) comprised of the Yatta Plateau which is a prominent escarpment rising more than 100m above its surroundings and ascending at a steep slope. Plant cover on the Yatta Plateau is dense: 40-80% shrub cover and 20-50% grass cover, thus not overlapping with the other plant-cover based habitats. To avoid pseudo-replication of habitat data caused by all members of a social group (elephants within 1-5 body distances from one another) being in the same habitat type, a single habitat type was recorded for each social group, and used as one record.

Seasonality

To evaluate whether the translocated elephants' behavior and physiology changed over time and to examine whether these measures converged with those of the local population over time, all data were assigned to five seasons. Seasons were defined based on known seasonal patterns of Tsavo East National Park (van Wijngaarden, 1985), on rainfall data collected by the Tsavo East Research Station throughout the study period, and on plant greenness. Rainfall data were collected monthly from 22-26 storage rain gauges distributed throughout Tsavo East National Park. The average rainfall collected from these rain gauges during this study is shown in Figure 2.1. Plant greenness was assessed during each elephant sighting on a scale of 0-3 based on the percentage of plants that were green (0: 0-25%; 1: 25-50%; 2: 50-75%; and 3: 75-100%). Plants became green or desiccated a few weeks after rainfall began or stopped, and therefore wet seasons were considered to begin only a few weeks after the rains started, and dry seasons began a few weeks after the rains stopped. Dry seasons were defined as months with lower than average rainfall and average plant greenness of 0-1, and months with high rainfall, following months of low rainfall, if plant greenness remained 0-1. Wet seasons were defined as months with higher than average rainfall and average plant greenness of 2-3, and months with low rainfall, that followed months of high rainfall, if plant greenness remained 2-3. The five seasons assigned were: 1) First long dry season (LD05) during which the elephants were translocated: September – October 2005; 2) Short wet season (SW05): November – December 2005; 3) Short dry season (SD06): January – February 2006; 4) Long wet season (LW06): March-May 2006; and, 5) the second long dry season (LD06) at the end of which the study ended: June – September 2006 (Figure 2.1).

Statistics

Body condition was analyzed using mixed ANOVA. Season, sex, and whether an elephant was translocated or local were fixed effects in the model. To control for repeated measures caused by the dependence of group members on the activities of one another and thus potentially the dependence of their body condition, elephants within 1-5 body lengths of one another were assigned to be in the same group. This group assignment and the interaction group*season were included as random effects in the model. Since no interactions among the fixed effects were significant, they were not included in the final model (Engqvist, 2005).

Data on mammary gland condition were analyzed using mixed ANOVA. Date and whether a female was translocated or local were fixed effects in the model. The identity of the female was included as a random effect in the model to control for repeated measures of the same female. None of the interactions among the model components were significant and therefore they were not included in the final model (Engqvist, 2005).

Data on stress hormones were analyzed using a general linear model (GLM). The model included the following effects: whether an elephant was local or translocated, age class (calf (0-5), juvenile (5-15), and adult (>15)), sex (male or female), season (wet or dry), and number of days in ethanol - to include any storage effects on the samples in the model. No random effects were included in the model because samples were obtained only from one member of a social group and elephants were not sampled more than once. Since no interactions among the effects of the model were statistically significant, they were not included in the final model (Engqvist, 2005).

The differences between the behavior and habitat use of translocated and local elephants were examined using a chi-square test. The estimated probability distributions for the behaviors or habitats during each season were compared between the local and the translocated elephants. For example, the estimated probability distribution of observations in each habitat (bush, bush-grass, perm-river, and hills) during season LD05 for the translocated elephants was compared to the estimated probability distribution of observations in each habitat for the local elephants, using a chi-square test.

All statistical analyses were conducted using the statistical software JMP (SAS institute, NC, USA).

Results

Of the 150 translocated elephants, 76 (51%) remained in Tsavo East. Fifty-seven of the translocated elephants that remained in Tsavo East were sighted more than three times throughout the study, indicating that they probably settled in Tsavo East (Table 2.1). Eleven translocated elephants did not stay in Tsavo East; of these, six returned to Shimba Hills, the source site for the translocation, three moved to Tsavo West, and two went to the coast, but not back to Shimba hills, and were shot near Malindi by the problem animal control unit (PAC) (Table 2.1). The fate of 41 (27%) of the translocated elephants is unknown. Twenty four of the translocated elephants (16%) died. Causes of death included poaching (n=1), shooting by PAC (n=2), and dying during the translocation itself (n=6). Twelve calves went missing and presumably died, and three individuals died of unknown causes (Table 2.1). All deaths of translocated elephants occurred within 55 days of release. Missing calves that were presumed dead (probably dead calves) disappeared within the first 1.5 months after translocation and no calves disappeared after that time. More translocated adult males and calves died than expected based on their proportion in the translocated elephant population, and fewer adult females and juveniles died than expected based on the age and sex distribution of the translocated elephants (Chi square: P=0.0009, Figure 2.2).

A comparison of the death rate of adult translocated elephants with that of the local elephant population in Tsavo East, revealed that adult translocated elephants had a greater probability of dying than local elephants (binomial distribution: P=0.03). Of the 103 translocated elephants whose fates were known and who did not die during the translocation, four adults died after the translocation. The estimated death probability of local elephants in Tsavo East was calculated to be 0.012 (77 dead elephants in a population of 6395) ($P_{\text{binomial}} = f\,(4; 103, 0.012) = 0.03$).

One translocated female gave birth to a calf in Tsavo East. The female and her calf were sighted six months after release when the calf's age was estimated to be one month. This finding indicates that the translocation did not completely disrupt ongoing pregnancies. Elephants have a long gestation period (22 months) and therefore additional calves conceived in Shimba Hills might have been born after this study ended. On the other hand, since it is difficult to observe and record evidence for premature pregnancy termination in elephants, the number of lost fetuses due to the translocation cannot be evaluated using observational data alone.

Body condition

A comparison of body condition between adult translocated elephants and local Tsavo adults (N=544), revealed a statistically significant difference between the two populations. Season, sex, and whether an elephant was translocated or local were all found to be significant effects in the mixed ANOVA model (Table 2.2). Although body condition of both translocated and local elephants fluctuated seasonally, with slight improvement during the wet seasons, body condition scores of the local elephants were higher than those of the translocated elephants throughout the study period, independent of season ($P=0.04$, Table 2.2, Figure 2.3). The only seasonal difference found to be statistically significant was the difference in body condition between the first dry season (LD05) and all other seasons ($P<0.001$, Table 2.2) with body condition improving after LD05. Females had a significantly poorer body condition than males ($P<0.001$, Table 2.2). The random effect ‘group’ accounted for 24.2% of the model’s variance, indicating there was variation in body condition between elephant groups but that elephants from the same group had similar body condition, as might be expected. The ‘group*season’ random effect interaction accounted for 10.6% of the model’s variance, indicating that the response of body condition to seasonal change differed depending on group identity.

Translocated females’ mammary glands were statistically significantly less full than those of the local Tsavo females. Whether a female was translocated or local had a significant effect in the model ($F_1=46$; $P<0.0001$; $N=168$). Date and the identity of the female were not statistically significant (date: $F_1=0$; $P=1$; identity: $T_6=1.98$; $P=0.09$). Thus, neither changes in mammary gland condition over time nor individual variation in mammary gland condition were detected in this analysis. The lack of change in mammary gland condition over time could have been the result of the short study period and long elephant gestation period. Changes in mammary gland condition depend on calf presence (B. McKnight, personal communication) and elephants’ gestation period is 22 months whereas the duration of this study was one year.

Stress hormones

No significant difference was found between the corticosterone levels of the translocated elephants and those of the local Tsavo elephants. Age class was the only statistically significant effect in the GLM model ($p=0.002$, Table 2.3). Adult elephants had significantly higher corticosterone levels than juveniles and calves (contrast analysis, $T=3.68$, $p<0.001$), but differences in corticosterone levels between calves and juveniles were not detected (contrast analysis, $T= -0.39$, $P=0.69$). Season and sex were not significant effects in the model (Table 2.3). Despite the non-significant effect of whether an animal was translocated or local on its corticosterone levels, the sample size in this study was large enough to provide sufficient power for determining that this non-significant result was not a type 2 error. A power analysis based on the sample size and SD obtained in this study ($N=38$, $SD=13.52$) and an effect size of 10 Ng/g based on the extent of seasonal effects on corticosterone levels found in Foley et al. (2001) produced a power of 0.99 at alpha=0.05. In fact, given the sample size and SD of this present study, an effect greater than 6.5Ng/g could have been detected at a power of 0.82 or higher and at alpha=0.05.

Behavior

The time translocated elephants spent foraging, walking, and standing differed from that of the local Tsavo elephants initially, but these differences disappeared over time. During the translocated elephants' first dry season in their new habitat (LD05) they spent more of their time standing, and less time foraging than the local elephants (Chi square; $P=0.012$, Figure 2.4). No statistically significant difference was found between the time translocated and local Tsavo elephants spent foraging, standing, and walking after the first dry season (Chi square; SW05: $P=0.51$; SD06: $P=0.68$; LW06: $P=0.22$; and LD06: $P=0.63$, Figure 2.4). Thus, over time the translocated elephants' behavior converged with that of the local population.

Habitat use

Habitat use of the translocated elephants differed significantly from that of the local Tsavo elephants throughout the study. During all seasons of the study, a statistically significant difference was found between the time allocated by the translocated elephants to different habitats and the local elephants’ time allocation to the different habitats (Chi square; LD05: $P < 0.0001$; SW05: $P < 0.0001$; SD06: $P=0.008$; LW06: $P < 0.0001$; LD06: $P < 0.0001$, Figure 2.5). Translocated elephants spent more of their time in hills and near permanent rivers than did the local Tsavo elephants, and less time in bush habitat than did the local elephants, but no difference was observed between the time spent by locals or translocated elephants in the bush-grass habitat (Figure 2.5). Thus, the translocated elephants’ habitat use was different from the local elephants’ habitat use, and did not change over time.

Discussion

Mortality rate of adult translocated elephants was significantly higher than that of the local Tsavo population. All translocated elephant deaths occurred within two months of release, suggesting that most deaths could be attributed either directly or indirectly to the translocation procedure and to the lack of familiarity of the translocated elephants with the new habitat. More males died than expected, based on their proportion in the translocated elephant population whose fate is known, possibly due to encountering human settlements during their long excursions away from the release site (see also Chapter 1). All translocated adult males that died after release were shot by humans: the KWS problem animal control unit shot two adult males near the coast, and farmers protecting their crops at the park boundary shot one elephant with a poison arrow. In addition, more translocated calves died after release than expected, according to their proportion in the population of translocated elephants whose fate is known (14 of 49), perhaps because of their high dependence on their mothers’ milk. The translocation was performed toward the end of the long dry season when little grass or bush foliage was present in Tsavo East, the release site, and vegetation overall was very dry. The combination of an unfamiliar environment and its dry condition likely affected females’ milk production, as supported by our finding that mammary glands of translocated females were significantly emptier than those of local females, possibly leading to the high mortality of translocated calves.

The physiological measures I assessed provided conflicting results. The difference in body condition between translocated elephants and local elephants throughout all seasons of the study supports the idea that arriving at a novel environment may have negative effects on newcomers. However, despite the significant difference in body condition, no significant difference was detected in the corticosterone metabolite levels between translocated and local elephants. The lack of difference in corticosterone levels may be related to the timing of sampling. A recent study on the fecal glucocorticoids of working African elephants showed an elevation in GC immediately after transporting the elephants to a novel habitat (Millspaugh et al. 2007). This increase in fecal GC levels subsided within 1-3 months and reached the GC levels of local wild elephants (Millspaugh et al. 2007). The first fecal sample collected in our work was obtained a month after the elephants were released. Thus, it is possible that if a peak in corticosterone occurred due to the translocation procedure, our fecal corticosterone sampling regime prevented us from detecting such a peak. Still, our finding that beyond a month post-release there was no detectable difference in corticosterone metabolites between the translocated and local elephants, at a high statistical power, implies that the translocation and the arrival to a novel environment did not induce long-term stress on the translocated elephants. Knowing that drastic environmental changes induced by translocations may not lead to heightened long-term stress is valuable since long-term stress may lead to memory and immune system dysfunction which may have great consequences to animals' fitness (Teixeira et al. 2007).

The absence of a significant difference in corticosterone metabolites between the translocated and local populations may also be a result of behavioral convergence. The only season during which a significant difference was found between the behavior of the translocated and the local elephants was the first dry season of the study. After this first dry season the translocated elephants and the local elephants spent similar proportions of their time foraging, walking, and standing. This finding may explain the similarities in corticosterone levels since an animal's behavior can influence its physiological condition through allostasis - achieving physiological stability through behavioral change (McEwen and Wingfield 2003; Wingfield 2005). Thus, the translocated elephants' convergence in behavior toward that of the local elephants' could have mediated the changes in the translocated elephants' physiology.

Persistent differences in habitat use between the translocated and the local elephants may be a result of the translocated elephants' preference for certain habitats or a result of competition leading to spatial partitioning. The source site for the translocation, Shimba Hills, is very hilly and its vegetative cover is mostly forest with open grasslands and grassed bushlands (Kahumbu 2002), similar to the bushed grassland and hills habitats in Tsavo, which the translocated elephants used post-translocation. Thus, the translocated elephants could have preferred using familiar habitat types at the release site. Alternatively, the differences in habitat use between locals and translocated elephants could have been the result of competition between the two populations and a mechanism for avoiding one another (Chapter 3). It is not clear whether the translocated elephants' habitat use was a result of their preference for familiar habitat features or a result of competition with the local population. Still, the fact that habitat use remained different between translocated and local elephants throughout the study period but social association with locals (when translocated and locals were in the same habitat) increased over time (Chapter 3) suggests that the translocated elephants' habitat use was a result of their preference for familiar habitat and not due to competition.

Overall, the translocated elephants appear to have acclimated to the novel environment over time. Their behavior converged with that of the local elephants, they found habitat that is similar to their source site, and there was no long-term elevation in stress hormones. Nonetheless, the body condition of translocated elephants was significantly worse than that of the local population throughout the entire study. Still, body condition did slightly improve over time, as suggested by the significant seasonal effect showing an improvement in body condition when comparing the first dry season to all other seasons following it. Body condition may take longer to change and adjust than behavior and hormone levels, possibly explaining the different results obtained using different assessment methods. Furthermore, the initial death rates of adult translocated elephants were higher than those of the local Tsavo population, and all translocated elephant deaths occurred very soon after release. Thus, in future translocations, translocation timing, release site location, and individuals targeted for the translocation should be chosen carefully: times of year when forage is readily available should be considered; release sites should be located far from human settlements to prevent human-elephant conflict that may lead to elephant mortality; and elephants with high mortality rates (adult males and young calves) should not be targeted.

This study presented and utilized non-traditional assessment measures for translocation success, such as behavior and physiology. These assessment methods can supplement or serve as proxies for long-term survival and reproductive success, when those cannot be obtained or when rapid evaluation for management purposes is needed. Furthermore, I used data from a local population as a baseline for comparing the biological measures of the translocated animals to further evaluate the outcomes of the translocation. The rate of convergence with a local population can indicate the extent to which translocated animals acclimate to their new environment. I hope that future studies of translocations will implement the novel assessment techniques employed here.

Behavior, physiology and a comparison of these measures to a resident population can provide information on the acclimation process of translocated animals to the new environment into which they are released. This type of information is vital for understanding the factors contributing to translocation success and will surely assist in evaluating the outcome of future conservation actions.

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Table and figure legends

Table 2.1: Translocated elephants' fate by age class and sex: Number of calves (age class 0-5 year), juveniles (age class 5-15 years), and adults (age class >15 years) by sex, that died after release (including cause of death), remained in Tsavo East, left Tsavo East, and whose fate is unknown.

Table 2.2: Statistics of the mixed ANOVA for body condition: Results from the body condition statistical model's fixed effects are presented (DF=degrees of freedom) N=544. None of the interactions among the model effects were significant and therefore they were not included in the final model. The random effects, not shown here, were 'group' which accounted for 24.2% of the model's variance and 'group*season' which accounted for 10.6% of the model's variance.

Table 2.3: Statistics of the GLM for stress hormones: Results from the stress hormone statistical model's fixed effects are presented (DF=degrees of freedom) N=38. None of the interactions among the model effects were significant and therefore they were not included in the final model.

Figure 2.1: Rainfall and seasons in Tsavo East National Park: Average (± SE) rainfall (mm) obtained from 22-26 rain gauges distributed throughout Tsavo East National Park, by month, during the years 2005 (left of the dashed line) and 2006 (right of the dashed line), for the period during which this study was conducted. Season definitions are indicated under months: LD05 - long dry season in the year 2005; SW05 – short wet season in 2005; SD06 – short dry season in 2006; LW06 – long wet season in 2006; LD06 – long dry season in 2006.

Figure 2.2: Translocated elephants' death by age and sex: Observed (black) and expected (white) number of translocated elephants that died during and after the translocation by sex and age class. Expected values were calculated based on the proportions of adult males, adult females and juveniles, and calves in the population of translocated elephants whose fate was known. Differences between observed and expected were statistically significant (Chi square; $P<0.001$).

Figure 2.3: Translocated and resident elephants' body condition over time: Average (± SE) body condition of adult translocated elephants (black circles) and local Tsavo elephants (white circles) throughout the study period, by season. Season notation as follows: LD05 - long dry season in the year 2005; SW05 – short wet season in 2005; SD06 – short dry season in 2006; LW06 – long wet season in 2006; LD06 – long dry season in 2006. Differences between translocated and local elephants were statistically significant for all seasons (see Table 2).

Figure 2.4: Translocated and resident elephants' behavior over time: Proportion of observations during which translocated elephants (black circles) and local Tsavo elephants (white circles) were seen foraging (a), standing (b), or walking (c) throughout the study period, by season. Season notation as follows: LD05 - long dry season in the year 2005; SW05 – short wet season in 2005; SD06 – short dry season in 2006; LW06 – long wet season in 2006; LD06 – long dry season in 2006. Only differences in behaviors between translocated and local elephants during LD05 were statistically significant (Chi square; LD05: P=0.012; SW05: P=0.51; SD06: P=0.68; LW06: P=0.22; and LD06: P=0.63).

Figure 2.5: Translocated and resident elephants' habitat use over time: Proportion of observations during which translocated elephants (black circles) and local Tsavo elephants (white circles) were seen in the different habitats: hills (a), permanent rivers (b), bush (c), or bush-grass (d) throughout the study period, by season. Season notation as follows: LD05 - long dry season in the year 2005; SW05 – short wet season in 2005; SD06 – short dry season in 2006; LW06 – long wet season in 2006; LD06 – long dry season in 2006. Differences between translocated and local elephants in habitat use were statistically significant for all seasons (Chi square; LD05: P< 0.0001; SW05: P< 0.0001; SD06: P<0.01; LW06: P< 0.0001; LD06: P< 0.0001).

Table 2.1

Age class	**Calves**		**Juveniles**		**Adults**		
Sex	**males**	**females**	**males**	**females**	**males**	**females**	**Total**
Died during the translocation	1	0	1	1	2	1	**6**
Poached in Tsavo East	0	0	0	0	1	0	**1**
Shot by PAC on the coast	0	0	0	0	2	0	**2**
Probably dead calves	3	9	0	0	0	0	**12**
Died in Tsavo - reason unknown	2	0	0	0	0	1	**3**
Seen in Tsavo East > 3 times	5	8	11	1	6	26	**57**
Seen in Tsavo East < 3 times	3	2	2	3	1	8	**19**
Returned to Shimba Hills	1	1	0	0	2	2	**6**
Moved to Tsavo West	0	1	0	0	1	1	**3**
Unknown	8	7	3	5	5	13	**41**
Total	**23**	**27**	**17**	**11**	**20**	**52**	**150**

Table 2.2

Fixed effects	**DF**	**F Ratio**	**P-value**
Translocated or Local	1	4.29	**0.04**
Season (LD05/SW05/SD06/LW06/LD06)	4	6.2	**<0.001**
Sex	1	14.11	**<0.001**

Table 2.3

Fixed effects	**DF**	**F Ratio**	**P-value**
Translocated or Local	1	0.05	0.82
Age class (Adult/Juvenile/Calf)	2	7.52	**0.002**
Sex	1	3.55	0.07
Season (Dry/Wet)	1	0.62	0.44
Time in ethanol	1	0.44	0.51

Figure 2.1

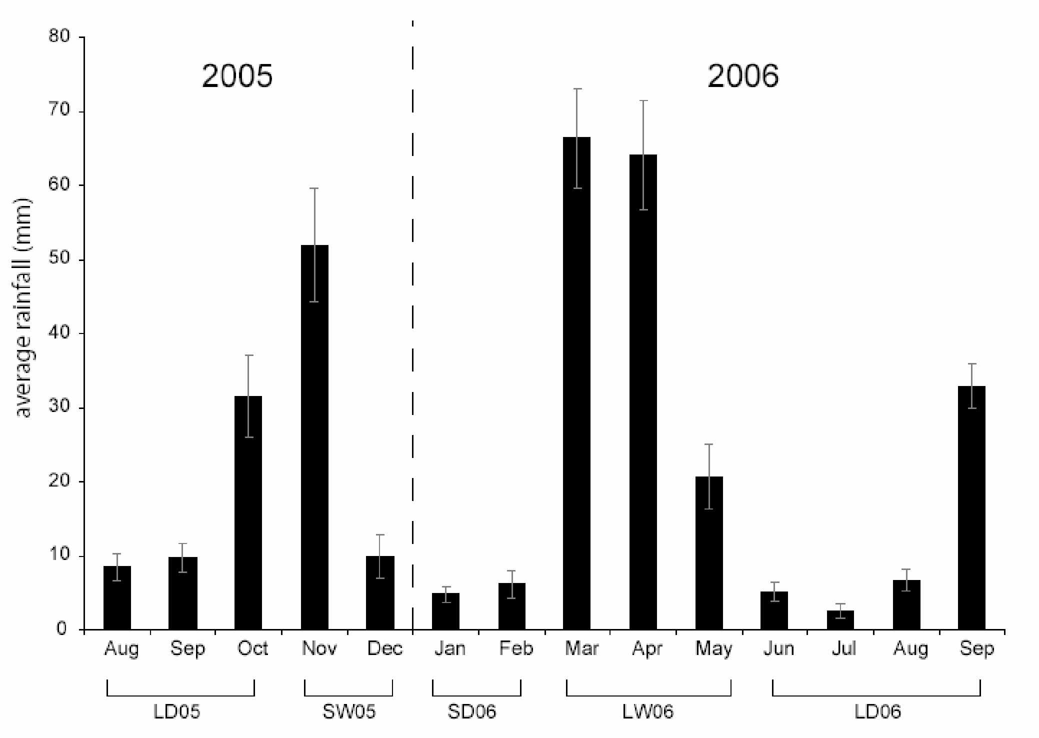


Figure 2.2

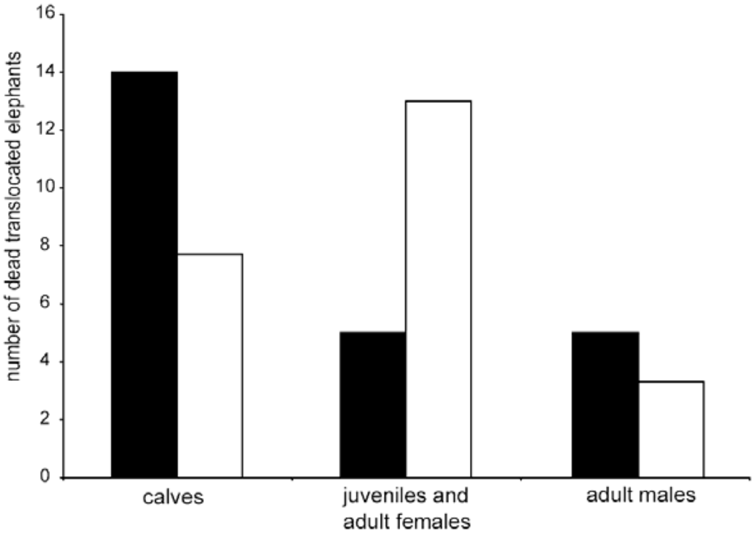
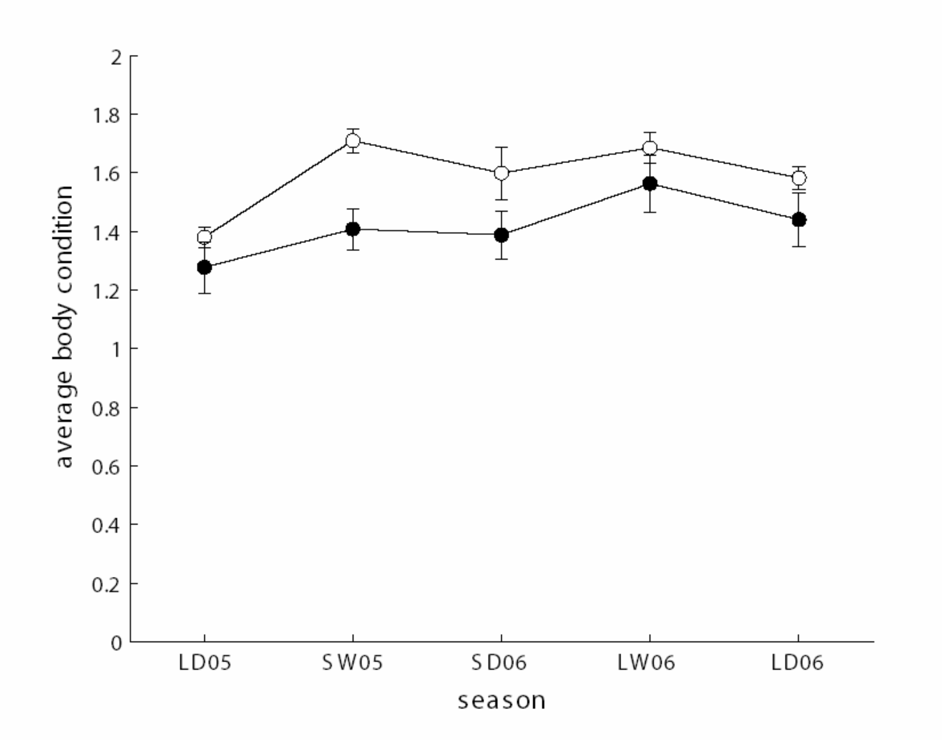


Figure 2.3


2
1.8
1.6
1.4
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1
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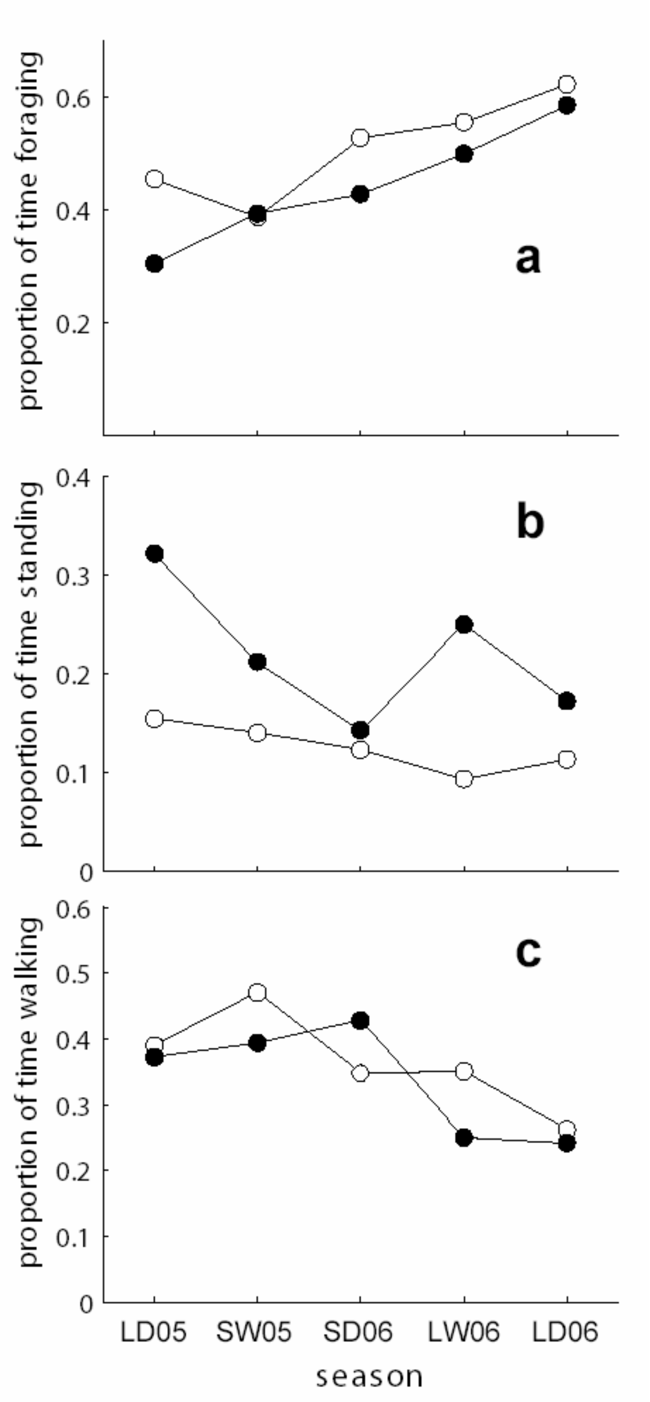
0.4
0.2
0
average body condition
LD05
SW05
SD06
LW06
LD06
season

Figure 2.4


proportion of time foraging
0.2
0.4
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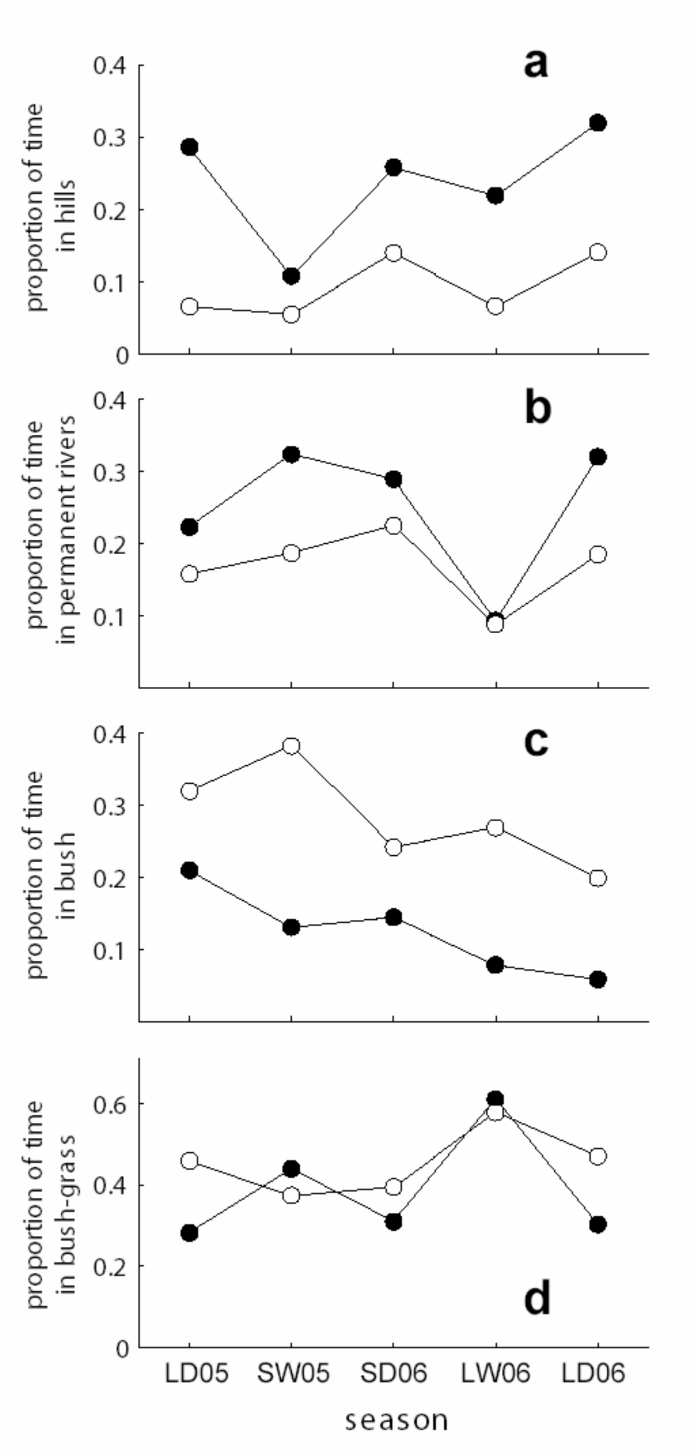
a
proportion of time standing
0
0.1
0.2
0.3
0.4
b
proportion of time walking
0
0.1
0.2
0.3
0.4
0.5
0.6
c
LD05
SW05
SD06
LW06
LD06
season

Figure 2.5


a
b
c
d
proportion of time in hills
proportion of time in permanent rivers
proportion of time in bush
proportion of time in bush-grass
0
0.1
0.2
0.3
0.4
0.6
LD05
SW05
SD06
LW06
LD06
season

Chapter 3

The relationship between social behavior and habitat familiarity in African elephants

Abstract

Social interactions with conspecifics can expedite animals' acclimation to novel environments, for example, through social learning about the new habitat. However, the benefits gained from social interactions in a novel environment may change as the habitat becomes familiar. Furthermore, with whom an animal interacts when arriving to a new environment, i.e., familiar conspecifics or knowledgeable unfamiliar residents, can influence the type of information an animal acquires about its new home. To examine the social dynamics and preferences of animals upon arrival to a novel habitat and how those preferences change as the habitat becomes familiar, I studied the social behavior of African elephants (*Loxodonta africana*) that were translocated into a novel environment. I found that overall social interactions of translocated elephants with conspecifics decreased with time spent in the new habitat. Furthermore, translocated elephants interacted significantly less than expected with local resident elephants and preferentially associated with other familiar, but not closely genetically related, translocated elephants. This social segregation between the translocated elephants and the local residents declined over time, suggesting that translocated elephants can integrate into an existing social setting. Little is known about the relationship between animals' social behavior and their familiarity with a habitat, despite the importance of such a relationship in the constantly changing world in which we live. I hope to provide here a foundation for future work on the relationship between social behavior and habitat familiarity.

Introduction

Animals often encounter novel environments, both naturally and due to human activities. Dispersing individuals encounter novel habitats while searching for a place in which to settle (Stenseth and Lidicker 1992; Stamps 2001), migrating animals locate novel habitats periodically (Mettke-Hofmann and Gwinner 2004), and foraging animals often come across novel food patches (Krebs and Inman 1992). Furthermore, animals are sometimes intentionally displaced by humans into novel settings, e.g., through translocations and reintroductions (Griffith et al. 1989; Sarrazin and Barbault 1996; Fischer and Lindenmayer 2000; Stamps and Swaisgood 2007), and by moving domestic herbivores while grazing (Burritt and Provenza 1997). Animals also encounter novel habitats due to human modifications to the environment, e.g., habitat loss (Sutherland and Dolman 1994), fragmentation (Ewers and Didham 2006), and introductions of non-native species (Schlaepfer et al. 2005; Strauss et al. 2006). In both natural and unnatural encounters with novel habitats, animals lack vital information regarding suitable forage, hiding locations, mating opportunities, and predators.

Social interactions with conspecifics can expedite animals' acclimation to a novel environment. The adaptive significance and ecological contexts of sociality have been studied extensively (Wilson 1975; Slobodchikoff 1988). However, very little is known about the significance of sociality when animals face novel environments. Many dispersing animals prefer settling with conspecifics rather than occupying empty territories (Cheney and Seyfarth 1983; Jack and Fedigan 2004, Griesser et al. 2008). Few studies discuss animals' group size preferences in a novel setting. One example comes from shoaling fish that prefer large groups to small groups of conspecifics when placed in a novel experimental setting (Agrillo and Dadda 2007). Still, only little is known about animals' social preferences when faced with a novel situation outside the lab, and even less is known about the dynamics of animals' social preferences as the novel habitat becomes familiar.

Several benefits can be gained from interacting with conspecifics in a novel habitat. For example, social learning is an important mechanism for gaining knowledge rapidly about the new environment. Interacting with several animals can provide abundant information about the surrounding habitat, while reducing the need for self-exploration (see reviews in Danchin et al. (2004); Dall et al. (2005); and Bonnie and Earley (2007), but see Isbell et al. 1993). Furthermore, the presence of conspecifics is known to facilitate learning novel tasks through copying or social enhancement (Day et al. 2001; Moscovice and Snowdon 2006). Associating with conspecifics in a novel environment can provide protection against unknown predators. Animals that are unfamiliar with their habitat are at a higher risk of predation than animals who are familiar with their surroundings (Isbell et al. 1990; 1993). Thus, newcomers may benefit from associating with conspecifics through the added vigilance of several nearby conspecifics. Finally, associating with conspecifics in a new habitat may provide protection against aggression from unfamiliar conspecifics, as seen in dispersing juvenile primates (Cheney and Seyfarth 1983; Jack and Fedigan 2004).

Associating with several conspecifics in a novel environment can entail costs in addition to the benefits mentioned above. For instance, resource competition is a well documented cost of group living (Koenig 2002; White and Warner 2007). When searching for patchy, depleting resources in a novel environment, a large group is less efficient at resource exploitation than solitary foragers. The time spent searching for resources is greater for a group than it is for solitary foragers due to the group's faster consumption and depletion of the resource (Beauchamp 2005). Furthermore, the presence of conspecifics can lead to agonistic interactions. When territorial animals arrive to a novel habitat they need to establish their territory, which may lead to agonistic interactions with conspecifics (Stamps 1994). As animals become familiar with their neighbors, aggression often decreases and therefore the costs of interacting with conspecifics may decrease as well (Temeles 1994).

The costs and benefits of social interactions and the relationship between these benefits and costs can vary depending on familiarity with a habitat. One hypothesis I suggest here is that animals benefit from interacting with conspecifics in a novel environment, but these benefits diminish as the habitat becomes familiar. An alternative hypothesis I suggest is that social interactions are costly to animals in a novel habitat but these costs are outweighed by the benefits of sociality as the habitat becomes familiar.

To understand the dynamics between the costs and benefits of sociality as a function of animals' familiarity with their habitat, one must examine animals' interactions with conspecifics when arriving at a novel habitat and monitor these interactions over time, as the environment becomes familiar. The first hypothesis suggested will be supported if the number of interactions with conspecifics decreases with time. An increase in the number of conspecifics an animal interacts with over time will support our second hypothesis. To my knowledge, no study has thus far investigated the relationship between social behavior and familiarity with a habitat.

In addition to the costs and benefits of interacting with conspecifics in a novel habitat, with whom animals interact is another important question. Animals can interact with unfamiliar local residents that are knowledgeable about the new habitat, or they can interact with familiar conspecifics that arrived with them to the new location. Interacting with familiar conspecifics and avoiding unfamiliar conspecifics have several advantages, regardless of whether a habitat is novel or not. For example, familiar conspecifics may assist one another when encountering aggressive unfamiliar conspecifics (Cheney and Seyfarth 1983; Jack and Fedigan 2004). The presence of familiar conspecifics is also known to reduce neophobia (Coleman and Mellgren 1994; Soma and Hasegawa 2004; Stowe et al. 2006). Furthermore, interacting with unfamiliar conspecifics can be costly. Unfamiliar individuals may carry unknown diseases and, it has been suggested that animals may be reluctant to interact with strangers to avoid disease transmission (Loehle 1995). Unfamiliar conspecifics can also be aggressive to one another (Cheney and Seyfarth 1983; Jack and Fedigan 2004; Goossens et al. 2005). Finally, learning about unfamiliar conspecifics can consume much time and energy that could be better spent on other activities such as getting to know a new habitat (Burman and Mendl 1999; 2002; Souza et al. 2006). Thus, overall, there are several benefits to interacting with familiar conspecifics and avoiding strangers. However, in a novel setting, an additional factor comes into play, the asymmetry in knowledge about the new habitat. The local, unfamiliar residents have information about the new habitat that familiar conspecifics might not have. The location of resident nesting sites and the residents' reproductive success are often used as an information source about the habitat's quality (Danchin et al. 2001; Part and Doligez 2003; Forsman et al. 2007). Such information about habitat quality cannot be obtained by interacting with or cueing in on familiar conspecifics who have recently arrived to the new habitat and have no prior information about it.

Social preferences, for unfamiliar knowledgeable local residents or for familiar conspecifics, are found in animals encountering novel habitats. Newly released translocated primates often leave the conspecifics with which they were released and integrate into local resident groups (Richard-Hansen et al. 2000; Vie et al. 2001; Goossens et al. 2005). Furthermore, conspecific cueing is successfully used when manipulating colonial birds into settling at a new habitat (Jeffries and Brunton 2001; Ward and Schlossberg 2004). On the other hand, accounts of translocated birds avoiding established residents exist (Clarke and Schedvin 1997), shoaling fish preferentially interact with familiar conspecifics and avoid unfamiliar conspecifics in a novel environment (Ward and Hart 2003; Griffiths 2003), and the formation of immigrant enclaves is well documented in humans arriving to a new country (Wierzbicki 2004). To determine whether animals prefer to associate with familiar or with unfamiliar conspecifics in a novel environment, one must study animals who are accompanied by familiar conspecifics when arriving at a novel environment which contains unfamiliar conspecifics.

Examining the social preferences of animals in a novel environment can provide important insights about social structure, social dynamics, and information acquisition. Animals' preferences regarding social interactions in a novel environment can also provide important information for basing wildlife management actions. Animals with a dynamic social system and capabilities for utilizing social information can provide an interesting system for studying the use of social interactions in a novel habitat.

African elephants' (*Loxodonta africana*) social dynamics provide an excellent opportunity for studying social preferences in a novel environment. Elephants live in a multiple tiered social system in which core family groups (second tier units) occasionally form bond groups (third tier social structures) (Moss and Poole 1983; Wittemyer et al. 2005). The genetic relatedness between elephants forming family groups, or second tier social units, is high, and the genetic relatedness between matriarchs forming bond groups, or third tier groups, is low (Archie et al. 2006). Elephants' social fission-fusion dynamics are governed by ecological factors (Wittemyer et al. 2005) and the formation of bond groups is thought to be important for gathering both social (Moss and Poole 1983) and ecological (Foley 2002) information, and can potently provide protection from predators (Wittemyer et al. 2005). Furthermore, elephants are highly intelligent mammals (Hart et al. 2008) that are capable of distinguishing between the vocal signatures of familiar and unfamiliar conspecifics (McComb et al. 2000; 2003). Thus, elephants' reliance on conspecifics for obtaining environmental information, their dynamic social system, and their extraordinary recognition abilities provide a suitable basis for examining whether they seek social interactions in a novel environment and whether they choose to associate with familiar or with unfamiliar conspecifics in the new habitat.

Recently, management of elephant populations has included translocating elephants from familiar to novel environments (Dublin and Niskanen 2003). This provided me with the opportunity to examine elephants' acclimation process to a novel environment. I first examined the change over time in overall social interactions between translocated elephants and conspecifics. A change in social interactions over time can inform about the relationships between familiarity with a habitat and the costs and benefits of sociality. I then examined genetic relatedness between translocated elephants to determine whether elephants released on the same day belonged to the same family group. Once family groups were defined, based on genetic relatedness, I was able to study the translocated elephants' bond group formation and determine whether the translocated elephants chose to associate with familiar or with unfamiliar conspecifics. Finally, I examined whether the translocated elephants' social preferences to local residents or translocated conspecifics persisted over time.

Methods

Translocation and release site

During September 2005, 150 African elephants were translocated from Shimba Hills National Reserve and Mwaluganje Elephant Sanctuary on the coast of Kenya (4°S to 4.3°S and 39.5°E to 39.3°E) to Tsavo East National Park (2.00°S to 3.70°S and 38.13°E to 39.30°E), a distance of 160 km. This translocation was part of the Kenya Wildlife Service (KWS) elephant management program's effort to decrease and possibly resolve human-elephant conflict in the vicinity of Shimba Hills. The translocation was carried out by KWS and was funded by the Kenya Government. All translocation procedures (anaesthetizing, transport, and tagging) were conducted by experienced KWS veterinarians and complied with IUCN's African elephant translocation guidelines (Dublin and Niskanen 2003). Elephant groups of fewer than 12 individuals were targeted for the translocation and were transported as intact units. Adult males were targeted based on their location and accessibility by road during the translocation and were moved in pairs. Translocating the 150 elephants took 32 days, during which 20 groups (average group size 6.8 elephants) and 20 adult males were moved.

The release site, Tsavo East, differs from the source site, Shimba Hills, providing a unique opportunity for examining the social behavior of elephants in a novel environment. Tsavo East is the largest national park in Kenya (13,950 km^2) and along with the adjacent Tsavo West National Park it forms the largest protected area in the country (20,812 km^2). The two Tsavo National Parks (East and West) are home to the largest elephant population in Kenya (approximately 9,000 individuals (Blanc et al. 2007)) while Shimba Hills, the source site, contains a small elephant population (approximately 600 individuals (Blanc et al. 2007)). Elephant density in Tsavo is 0.43 elephant per km^2 while elephant density in Shimba Hills is 2.4 elephants per km^2. This difference in elephant population density can potentially lead to a lower encounter rate between elephants at the release site than at the source site. In addition, ecological differences between the two sites provide a novel ecological situation for the translocated elephants. For example, the climate of Tsavo East is semi-arid, while Shimba Hills' climate is humid equatorial. During the rains, vegetation growth in Tsavo East is spatially more heterogeneous and unpredictable, relative to Shimba Hills (van Wijngaarden 1985).

Sightings post-translocation

During the translocation, all elephants were individually marked for post-translocation monitoring. All 150 elephants were tagged with yellow zip ties on their tails to distinguish them from the local Tsavo elephant population. Translocated elephants were also painted with a unique white number on their backs for individual identification. Natural ear marks and tusk shape were used for individual identification when the painted numbers were no longer visible (Moss 1996). The age of each translocated elephant was estimated, according to body measurements (back length and shoulder height) taken during the translocation and observations later in the field, based on Moss (1996).

The locations and behavior of translocated and local Tsavo elephants were recorded over a course of one year post-translocation. Road transects in Tsavo East were conducted using a vehicle four to five times a week, alternating between four different routes of similar length (50-70 km) on existing roads within Tsavo East National Park. All elephants sighted during the transects were noted. Data recorded for each individual elephant sighted included whether it was translocated or local, its sex and estimated age, distance to nearest neighbor in units of elephant body length, and location – longitude and latitude using a Geko 201 GPS unit (Garmin Ltd., USA). Elephant locations were recorded as the location of the observer's vehicle. Due to the dense vegetation, most elephants seen were in close proximity to the vehicle, thus the vehicle's position provided a suitable estimate for the observed elephants' location. Elephants within five body lengths of one another were all recorded to be in the same location. When translocated elephants were encountered, the individual identity of each group member was recorded and the observer remained with the elephants until they could no longer be seen (ranging from five minutes to two hours) while recording behaviors a*d libitum* and scan samples, when possible (Altmann 1974). A total of 3420 elephant sightings were recorded, of which 435 were of translocated elephants and 2985, of local elephants.

Proximity definition

All associations between individual elephants or between elephant groups (see distinction below) were defined as being within 500m from one another in a time window of two hours, based on the criteria used by McComb et al. (2000). These proximity criteria allowed sufficient time for elephants to either directly interact or to recognize the vocal signals of other individuals that were out of sight (McComb et al. 2000; McComb et al. 2003).

Overall proximity

To test whether the number of conspecifics in proximity to the translocated elephants changed over time, I calculated overall proximity for each sighting of a translocated elephant. Overall proximity is defined as the number of other elephants, translocated or local, in proximity (as defined above) to an observed translocated individual, for each of its sightings.

Association between translocated elephants

To quantify the association between translocated elephants I computed an association matrix using the simple ratio association index (Cairns and Schwager 1987; Ginsberg and Young 1992) which is often used in studies of elephant social behavior (McComb et al. 2000; McComb et al. 2001; Wittemyer et al. 2005). The simple ratio association index is calculated as $AI=N_{AB}/(N_{AB}+N_A+N_B)$ where N_{AB} is the number of times individual A was seen in proximity to individual B (see proximity definition above); N_A is the number of times individual A was seen without individual B; and N_B is the number of times individual B was seen without individual A. An association matrix was computed only for the translocated elephants and not for the local Tsavo elephants since individual identity information could not be recorded for these elephants due to their large numbers.

To quantify the association of each translocated individual with all other translocated elephants, weighted degree was calculated using Ucinet (Borgatti 2002). Weighted degree is an extension of the simple degree measure (number of nodes with which an individual node is connected in a network) that takes into account the weight of the connections (the strength of association). Weighted degree was calculated based on an association network of only translocated elephants older than five years since calves seldom leave their mothers (Wittemyer et al. 2005); including them would have disproportionately increased the weighted degree of females with calves.

Proximity to locals

To examine the social association between the translocated elephants and the local Tsavo elephants, their proximity to one another was calculated as the proportion of sightings for each translocated elephant in proximity to a local elephant: $P2L_i = N_{iL}/N_i$ where N_{iL} is the number of times translocated elephant i was in proximity to any local elephant (see proximity definition above); and N_i is the total number of times elephant i was seen. P2L was calculated only for elephants older than five years since calves' activities are strongly associated with their mothers' (Wittemyer et al. 2005) and therefore their P2L would have been the same as their mothers. Including calves in this analysis would have biased the average P2L towards that of females with calves.

Genetic analysis

To test whether translocated elephants released on the same day were family groups and whether elephants released on different days were unrelated, for further analysis of bond group formation, I examined the genetic relatedness between translocated elephants. During the translocation procedure, tail hairs were collected from 66 elephants while they were anesthetized. The follicles of these hairs were used for the DNA analysis. 17 Microsatellite loci from previous molecular work on elephant genetics were amplified using PCR. The microsatellites used were: FH126 from (Comstock et al. 2002), FH19, FH39, FH48, and FH67 from (Comstock et al. 2000); LafMS01, LafMS02, LafMS03, and LafMS04 from (Nyakaana and Arctander 1998); and LaT05, LaT06, LaT07, LaT08, LaT13, LaT16, LaT24, and LaT25 from (Archie et al. 2003). Details of DNA extraction and amplification can be found in Appendix A.

Genetic relatedness based on these microsatellites was estimated using Wang's estimator (Wang 2002), implemented in the program SPAGeDi (Hardy and Vekemans 2002). Wang's relatedness estimator is designed especially for dealing with highly polymorphic markers such as microsatellites, in populations where relatedness is unknown (Wang 2002) and provides a more accurate relatedness estimation than other commonly used methods such as Queller and Goodnight (1989) (see review in Oliehock et al. (2006)).

To test whether the association of translocated elephants with one another was related to their genetic relatedness, I computed an association matrix for individuals who were sighted in the field and whose DNA samples were obtained during the translocation (N=42 elephants). The association matrix was computed as described above using the simple ratio association index and the proximity definition above.

Association between groups: bond group formation

To evaluate whether translocated elephant family groups formed bond groups with other translocated elephants or with local conspecifics, the individual sightings were grouped into units equivalent to core familial groups also known as second tier units, described in Wittemyer et al. (2005). Translocated elephants captured and released on the same day were considered to be a family group (see relatedness results below to support this grouping method). Local elephant family groups were assigned based on spatial proximity since no genetic data were available for the local population. Local elephants within five elephant body lengths of one another were considered to be a family unit.

The number of group interactions, based on the proximity definition above, was summed for each of the following categories: TT - two translocated groups released on different days in proximity to one another; LL – two local groups in proximity to one another; TL - translocated groups in proximity to local groups; and T -translocated or L - local groups alone.

Permutation model

To test whether the number of observed encounters between elephant groups differed from an expected random encounter rate, a permutation model was used to produce an expected distribution for the number of interactions between elephant groups (Good 2005). The permutation shuffled group identity, local or translocated, at random, while preserving sighting location and time. This procedure controlled for the elephants' habitat choice, since sighting locations were not randomized, similar to the permutation models developed by Bejder et al.

(1998). In order to assume a well mixed population, in which each group‘s identity could be replaced with any other group’s identity, sightings used for the group interaction analysis were restricted to a 25km radius around the release site. This restriction is based on elephants’ movement abilities in natural populations of up to 50km a day (Douglas-Hamilton et al. 2005) and on the daily travel distances that translocated elephants exhibited (N P-W, pers. obs.).

1000 permutations were run and the mean values of the simulated TT, LL, TL, T, and L were calculated. These average values were compared with the observed values of these variables using a Chi Square test. Permutations and statistical analysis were implemented in Matlab (MathWorks Inc., MA, USA).

Change over time

To test if the translocated elephants’ social behavior changed over time, data from two dry seasons one year apart were compared. The long dry season in Tsavo East typically lasts from June to October (van Wijngaarden 1985). Data collected during this time window in 2005 were compared with data from the same time period in 2006. Elephant sightings for the first long dry season were obtained from September 1st 2005, the date on which elephants were first released, until November 21st 2005, when the rains began, providing three months of data. Sightings for the second long dry season were obtained from May 29th 2006, four weeks after the last rains and when vegetation began to dry and lose its leaves, and ended on October 2nd 2006 when the study ended, providing four months of data. In both these seasons a similar number of sightings were obtained (914 sightings in the 2005 long dry season and 1033 sightings in the 2006 long dry season). For each long dry season (2005 and 2006) the weighted degree and P2L were calculated for each translocated elephant, as described above.

Statistical analysis

To test whether overall proximity changed over time and to control for repeated measures of the same translocated individual, a random effects-mixed model was used. Number of days since release was a fixed effect in the model and elephant identity was a random effect in the model. The interaction between elephant identity and number of days from release was also included in the model as a random effect to examine whether any trends over time were a product of individual variation in overall proximity. To test whether elephants released on the same day interacted with one another more than expected at random, a Mantel test was used to compare the AI matrix with a release day matrix (a binary matrix assigning one to pairs released on the same day and zero to pairs released on different days). To determine whether observed association between groups differed from expected based on the permutation test, a chi-square test was used to compare the observed values with the average values from 1000 permutation runs. Relatedness between elephants translocated on the same day was averaged and compared to the average relatedness value between elephants translocated on different days using a Student's T-test. To examine the relationship between weighted degree and P2L, and to examine the relationship between AI and relatedness, a Pearson correlation coefficient test was used. To examine change in social behavior over time, the average weighted degree from 2005 was compared to that from 2006 using a Wilcoxon signed ranks test. Similarly, the average P2L for 2005 was compared with the average P2L in 2006 using a Wilcoxon signed ranks test. Statistical analyses were implemented in Matlab using its statistical toolbox (MathWorks Inc., MA, USA) and in the statistical analysis program JMP (SAS institute, NC, USA).

Results

Overall proximity of translocated elephants to conspecifics decreased with time (Random effects-mixed model: $R= -0.35$, $N=434$). Time since release and elephant identity were significant effects in the mixed model (time: $F_{1,207}=9.4$, $P=0.0025$; elephant identity: $T_{352}=6.31$, $P<0.0001$) but the interaction between them was not significant ($T_1= -0.96$, $P=0.51$). The significant elephant identity random effect suggests that there was individual variation among the translocated elephants in how fast their social interactions declined over time. However, the fact that the interaction between time and elephant identity was not significant indicates that overall, the translocated elephants' proximity to conspecifics decreased with time, despite individual variation.

Translocated elephants that were released on different days interacted with one another throughout the study period (Figure 3.1). Elephants released on the same day interacted with one another more than expected at random (Mantel test: $R=0.3$, $P< 0.01$). Groups released on different days interacted statistically significant more with one another than expected according to the permutation model (Chi square test: $X^2_4=743.26$, $P<0.001$; Figure 3.2).

Interacting translocated groups were not genetically related. Elephants released on the same day were significantly more closely related to one another than elephants released on different days (Student's t-test: T_{90}=-3.15, P=0.002; Figure 3.3). Relatedness between elephants released on the same day was, on average, X±SE=0.13±0.02, similar to the relatedness found between individuals forming a core family group in undisturbed African elephant populations (Archie et al. 2006). Thus, elephants translocated on the same day were most likely from the same family, supporting the grouping method I used for the translocated elephants in the permutation model. In contrast, average genetic relatedness between elephants released on different days was: X±SE=-0.02±0.003. In relatedness analysis using microsatellite data, negative relatedness values are interpreted as individuals sharing fewer alleles than expected at random based on a Hardy-Weinberg allele frequency, thus negative values indicate with high confidence that two individuals are unrelated (Konovalov and Heg 2008). In addition, the strength of social association between elephants released on the same day correlated positively and significantly with their relatedness (Pearson correlation: R=0.51, N=60 pairs, P<0.001) as one might expect based on previous work (Archie et al. 2006). However, the social association strength between translocated elephants that were released on different days did not significantly correlate with their relatedness (Pearson correlation: R= 0.29, N=32 pairs, P=0.1). Thus, interactions between translocated elephants released on different days were not mediated by genetic relatedness.

Translocated elephants interacted statistically significantly less with the local Tsavo elephant population than expected according to the permutation model (Chi square test: X^2_4=743.26, P<0.001; Figure 3.2). Moreover, a significant negative correlation was found between translocated elephant proximity to local Tsavo elephants and their weighted degree as a measure of their proximity to other translocated elephants (Pearson correlation: R= -0.28, N=66, P=0.02; Figure 3.4). In other words, the more a translocated elephant interacted with other translocated elephants, the less it interacted with the local elephant population, and vice versa.

Translocated elephants' preferential interactions with other translocated elephants, and their lack of interactions with local elephants, did not persist over time. The average weighted degree of translocated elephants decreased significantly between the long dry season of 2005 and that of 2006 (Wilcoxon signed ranks test: T=186, N=100, P<0.001; Figure 3.5a). Furthermore, the proximity of translocated elephants to local elephants was more frequent in the long dry season of 2006 than that of 2005 (Wilcoxon signed ranks test: T=1.5, N=16, P=0.01; Figure 3.5b). Thus, the translocated elephants' social preference and social structure changed over time, from a closed immigrant enclave to being integrated with the local elephants.

Discussion

Social interactions between translocated elephants and conspecifics decreased over time. This result supports our hypothesis that elephants benefit from interacting with conspecifics when arriving at a novel environment, but these benefits diminish as the habitat becomes familiar, leading to fewer interactions with conspecifics. The direct benefits and costs of sociality in a novel environment were not measured in this study but one suggestion could be that social learning played an important role in the elephants' information acquisition about their new home. This suggestion is based on previous work by Foley (2002) who provides evidence for the importance of social knowledge in elephants regarding information about their habitat. As time passed and the translocated elephants became familiar with the habitat, their need for social interactions to gain knowledge abut their new home probably decreased, and costs such as resource competition probably began to outweigh the benefits of interacting with conspecifics.

Translocated elephants retained their core family groups in the novel environment. This information is perhaps not surprising considering elephants' strong social ties and strong genetic relatedness within their family group – second tier social level (Wittemyer et al. 2005; Archie et al. 2006). Still, often enough, animals released together as a familiar group, split up (Armstrong and Craig 1995; Armstrong 1995; Jones et al. 1997; Richard-Hansen et al. 2000; Ostro et al. 2001), as was seen in some elephant groups in our study (Figure 3.1).

When examining the formation of bond groups – third tier social level, I found that translocated elephants formed bond groups with other, genetically unrelated, translocated groups and not with local resident elephant groups. These social interactions were statistically significantly different from the social interactions predicted by the permutation model. Thus, translocated elephants interacted more than expected with familiar conspecifics than with unfamiliar local residents. When considering elephants' extraordinary social memory (McComb et al. 2001; 2003), long distance communication abilities (Poole et al. 1988; McComb et al. 2003), the small size of the source site from which the elephants were translocated, and the ranging patterns of elephants at the source site (Kahumbu 2002), it is safe to assume that all translocated elephants were familiar with one another and that interactions between translocated elephants post-release reflected social bonds between individuals who are familiar with one another. I further found a negative relationship between translocated elephants' interactions with other translocated elephants and their interactions with local elephants (Figure 3.4). This finding shows that translocated elephants did not have a high interaction rate with both translocated elephants and local elephants, suggesting that translocated elephants had to choose between interacting with one type or the other.

Several explanations can be provided for the social segregation between the translocated and local elephants observed in this study. Aggression between unfamiliar elephant groups is one likely explanation. Elephants maintain a linear dominance hierarchy among family groups (Wittemyer and Getz 2007) and newcomers are not part of the established dominance hierarchy among the local residents. Indeed, on the two observations of direct interactions between a translocated group and local residents, the locals initiated an aggressive response towards the translocated group, supporting the suggestion that agonistic behavior had a role in separating translocated from local elephants. The low genetic relatedness among translocated elephants released on different days suggests that interactions between translocated groups did not provide inclusive fitness benefits. Still, other benefits of sociality and of interacting with familiar conspecifics could have led the translocated elephants to seek familiar conspecifics. Such benefits might include protection during encounters with local unfamiliar elephants, social learning, reduced neophobia, and facilitation of behaviors, such as habitat exploration, that are important for becoming acquainted with the new environment.

The costs of interacting with unfamiliar conspecifics (to both the translocated and the resident elephants) were probably greater than the benefits translocated elephants would have gained from interacting with the local residents to obtain information about the new habitat that other translocated elephants might not have had. In addition, it is possible that any added information the resident elephants possess about the habitat would be relevant only during severe drought years or other extreme environmental conditions (as seen in the use of knowledge by old matriarchs in the study by Foley (2002)). Thus, interacting with the local residents might have been irrelevant for gathering information about the habitat during the acclimation period of the translocated elephants to their new home.

The observed social segregation between translocated and resident elephants dissolved over time as the habitat became familiar to the translocated elephants. The association among translocated elephants immediately after release, during their first dry season in the new habitat, was significantly higher than their association with one another during the same dry season a year later. Furthermore, there were fewer interactions between translocated elephants and local residents during the first dry season immediately after release than during the same season a year later (Figure 3.5a,b). This result further supports the fact that social interactions are dynamic and change as a function of how familiar animals are with their habitat. At first, when the translocated elephants were unfamiliar with the new habitat, they associated primarily with familiar conspecifics. As time passed and they became familiar with the habitat these interactions subsided. Furthermore, as the translocated elephants became familiar with their new home, they probably also got to know the local resident elephants and began to interact with them more, maybe because agonistic encounters were not as prevalent as upon arrival to the new habitat. Thus, translocated elephants were able to socially integrate into an unfamiliar population when given enough time.

Despite the frequent exposure of animals to novel environments, animals' familiarity with their habitat has never before been considered a factor in determining the dynamics of animals' social behavior. This study shows that translocated elephants' interaction rates with conspecifics decrease as a novel habitat becomes familiar. This implies a dynamic relationship between the costs and benefits of sociality and habitat familiarity. Further work is still needed to examine the details of these cost-benefit dynamics, but the work presented here provides a foundation for future studies linking animals' social dynamics with their habitat familiarity. Furthermore, forming social enclaves in a novel environment by animals is a phenomenon that is very seldom documented. The ability of animals to sustain social bonds when moved into a novel habitat, as seen in the translocated elephants of this study, can provide important insights to both wildlife management actions and to the study of animal behavior in general.

Translocations and other wildlife management actions provide abundant opportunities for exploring the behavior of animals in novel settings, behaviors that are important during natural life stages such as dispersal and migration. It is likely that as the world continues to change due to human activities, more evidence for complex social dynamics in animals colonizing novel habitats will be revealed and more opportunities will open up for studying the function and mechanisms underlying their social preferences.

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Figure legends

Figure 3.1: Social network of translocated elephants. Network nodes represent individual translocated elephants and edges connecting the nodes denote the observed social association (AI) between connected elephants. Elephants that were released on the same date are represented in the same color. Node size denotes elephant age in four age class categories (from the smallest to largest: 0-5; 5-15; 15-30; 30+). Node shape indicates sex (□ male; ○ female). Edge thickness denotes strength of association, the darker and wider the edge, the stronger the association (larger AI) between the two elephants. This network graphical representation was created using the program Cytoscape (http://cytoscape.org).

Figure 3.2: Observed group proximity compared with random permutation model results. Log of the ratio between the observed and expected (as computed by the permutation model) number of times translocated elephant groups were seen alone (T); translocated groups were in proximity to other translocated groups released on a different day (TT); translocated groups were in proximity to local elephant groups (TL); local groups were in proximity to other local groups (LL); and local groups were seen alone (L). Differences between observed and expected values are significant $p<0.001$, Chi square.

Figure 3.3: Genetic relatedness between and within translocated elephant groups. Average relatedness (r values) for elephant pairs released on different days – between groups (N=1649 pairs) and for elephant pairs released on the same day – within groups (N=181 pairs). Error bars denote standard error. Difference between the average within group and between group relatedness is statistically significant: p-value=0.002, T-test.

Figure 3.4: Relationship between proximity to locals and weighted degree. Proximity to locals is the proportion of sightings in which a translocated elephant was in proximity (within 500m and 2 hours) to local elephants. Weighted degree is the sum of AI values for each translocated elephant. Data presented only for elephants older than 5 years that were sighted in the field post-translocation (N=66). Dotted line is the linear regression fit to the data. Negative trend is significant: $r=-0.23$, $p=0.02$, Pearson correlation.

Figure 3.5: Change in weighted degree and proximity to local elephants over time. (a) Average weighted degree as a measure of interaction rate between translocated elephants was statistically significantly higher during the first long dry season (2005) than it was during the long dry season a year later (2006) ($p<0.001$, Wilcoxon signed ranks test). (b) Average proportion of sightings of translocated elephants in proximity to local elephants (P2L) was statistically significantly lower during the first dry season (2005) than it was during the long dry season a year later (2006) ($p<0.01$, Wilcoxon signed ranks test). Error bars indicate standard errors.

Figure 3.1

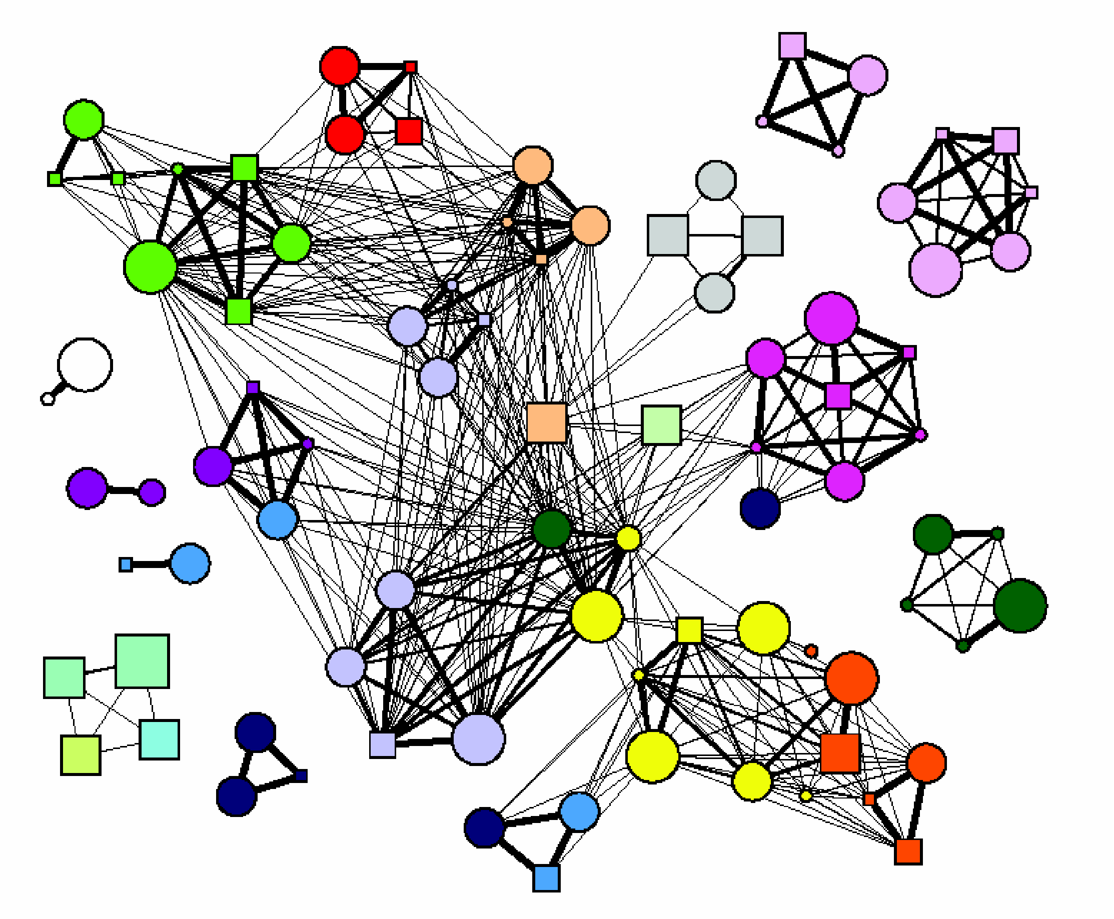


Figure 3.2

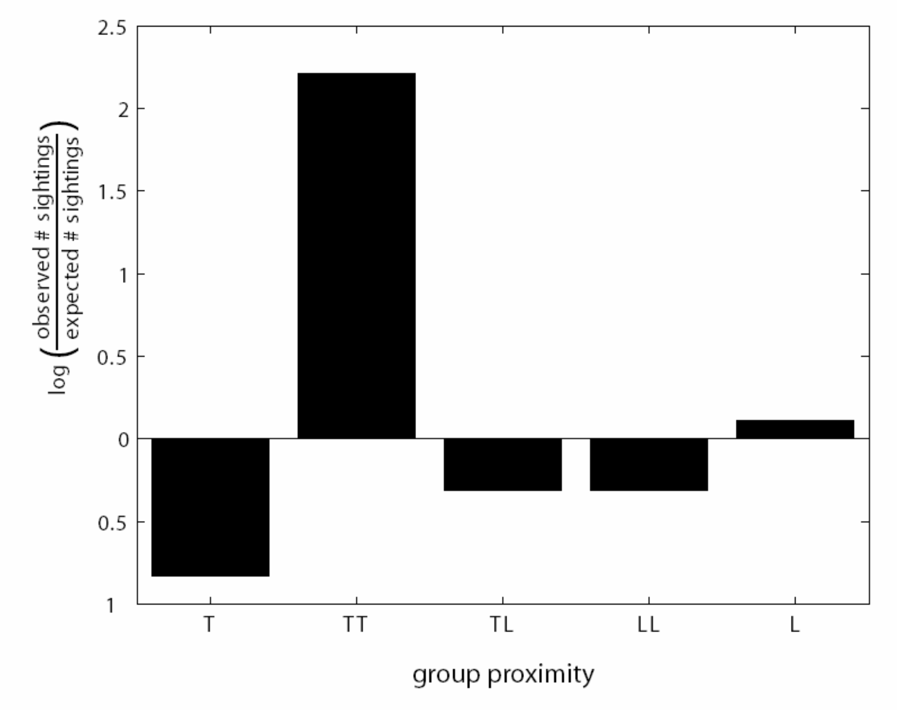


Figure 3.3

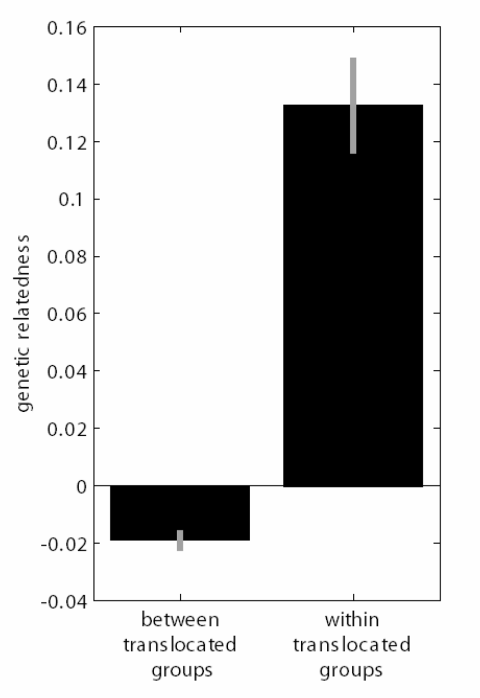


Figure 3.4

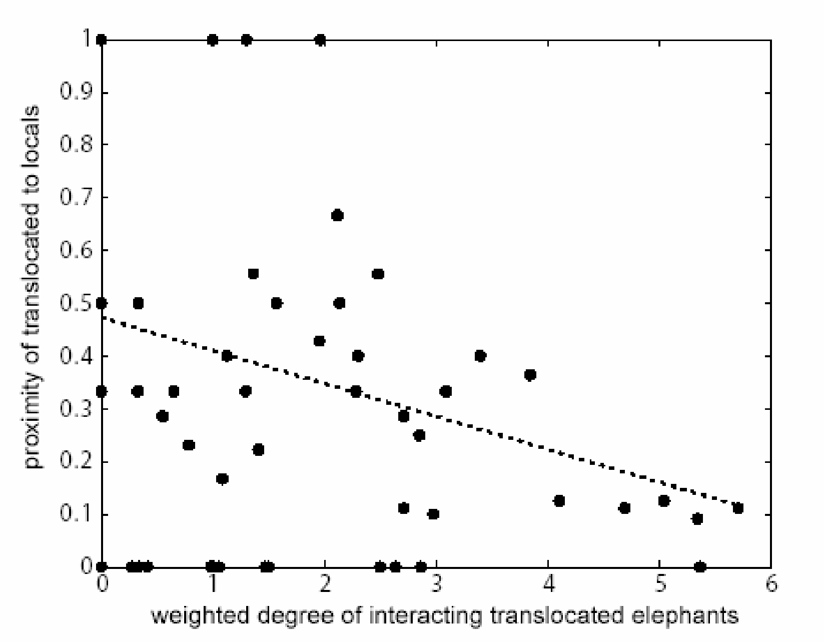
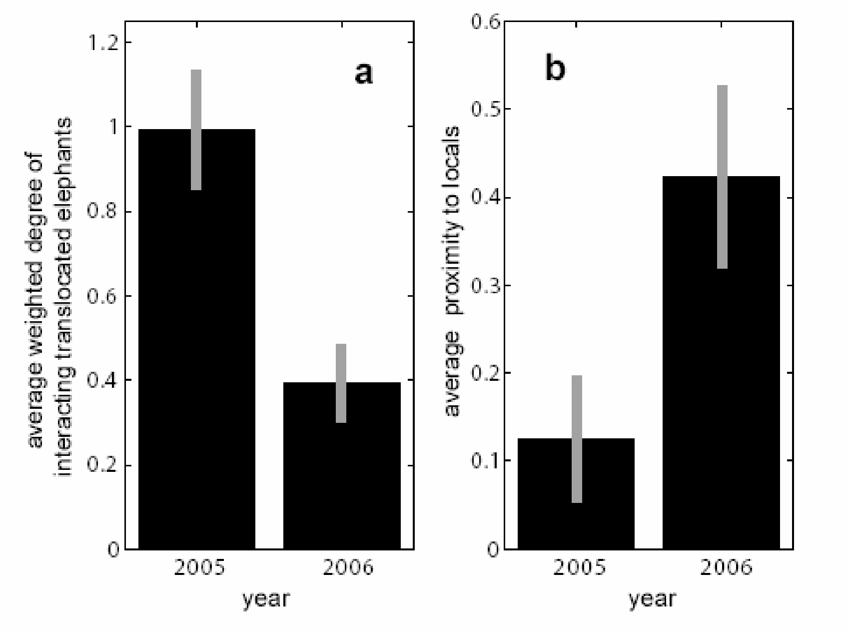


Figure 3.5



Appendix A

Genetic analysis: details of DNA extraction and amplification

DNA was extracted from each root using 100ul of a hair lysis solution consisting of 2.5 mM $MgCl_2$, 1X PCR buffer (Applied Biosystems), 0.5 µLTween 20, and 0.5 µL protienase K at 20 mg/µL. Reverse primers and forward primers labeled with 6-FAM fluorescent dye were purchased from Sigma Genosys. Primers labeled with PET, VIC and NED fluorescent dyes were purchased from Applied Biosystems. Primers were optimized and multiplexed when possible.

Microsatellites were amplified in 12.5 µL reactions on an MJ Research PTC-100 thermalcycler with a *hotstart* procedure of incubating the DNA and the primers at 95ºC for 5 min and at 80ºC for 10 min; addition of the further reagent mix (see table 3.1), followed by one of three cycling protocols. 56 w/Hot: 35 cycles of incubation at 95ºC for 30 s, at 56ºC for 30 s and at 72ºC for 45 s; a final extension step at 72ºC for 10 min. TD 56: the touch down protocol described in Archie et al., 2003. Or TD 52: the same touch down protocol modified to start at 62 ºC and the 30 regular cycles annealing at 52 ºC. The length of the PCR fragments was determined by capillary electrophoresis (ABI 3730, Applied Biosystems) relative to an internal size standard (500 LIZ™, Applied Biosystems) and using the STRand (Hughes, 2000) software.

Reagent mixes provided in table: 3.1. 1x PCR buffer, 2.5mM $MgCl_2$ (Applied Biosystems), 200 µM dNTPs (Roche), 0.5 U *Taq* DNA polymerase (ABgene) and sterile water. 2. 1x PCR buffer, 1.5mM $MgCl_2$, 200 µM dNTPs, 0.5 U *Taq* DNA polymerase and sterile water. 3. 1x PCR buffer, 1.6mM $MgCl_2$, 200 µM dNTPs, 0.5 U *Taq* DNA polymerase, 0.8 M Betaine (Sigma) and sterile water. 4. 1x PCR buffer, 0.8mM $MgCl_2$, 200 µM dNTPs, 0.5 U *Taq* DNA polymerase, 0.8 M Betaine and sterile water. 5. 1x PCR buffer, 1.6mM $MgCl_2$, 200 µM dNTPs, 0.5 U *Taq* DNA polymerase, 0.8 M Betaine, 0.08ug/ul BSA (Sigma) and sterile water.

Table 3.1: Microsatellites used for genetic analysis

Microsatellite name	T_a	Cycling protocol	Reagent mix	Primer concentration		Sequence	Source
FH126	56	TD	3	0.7	F-	TCTGATAGGCTGGTGTAAGCTG	Comstock, et al.,2002
					R-	TCTCTCCTCCCTTCCCTCTC	
FH19	56	W/Hot	1	0.3	F-	GAAGCTCATGGTCAAGGTCAC	Kenine, et al., 2000
					R-	CTGCATACTCATCGAAGTCACC	
FH39	56	W/Hot	1	0.09	F-	GTATTCCTGGGCATTCCATG	Kenine, et al., 2000
					R-	CTTGGAATATGACCCTGTTTG	
FH48	56	TD	3	0.8	F-	GAGTCTCCATAATCAAGAGCG	Kenine, et al., 2000
					R-	CCTCCCTGGAATCTGTACAG	
FH67	56	W/Hot	1	0.3	F-	GCTTCTCTAGAAATGTGTATGC	Kenine, et al., 2000
					R-	GGCGTATAGGATAGTTCCAC	
LafMS01	56	TD	3	0.05	F-	GTCGTCGCCCGAGCACAGTCGCT	Nyakaana & Arctander, 1998
					R-	ACCTGATTCAGGGAGCACGG	
LafMS02	56	TD	3	0.5	F-	GAAACCACAACTTGAAGGG	Nyakaana & Arctander, 1998
					R-	TCGCTTGTAAGAAGGCGTG	
LafMS03	52	TD	3	0.25	F-	CATATGAACATACCGGAAC	Nyakaana & Arctander, 1998
					R-	GAAACTCCTCGAGTAGTAGAA	
LafMS04	56	TD	3	0.3	F-	GGGACACATGTGTGCATAA	Nyakaana & Arctander, 1998
					R-	TTATGTCTGCATAGACAGGTTGG	
LaT05	56	TD	5	0.7	F-	CACCACCCATCCATCTGT	Archie, et al., 2003
					R-	TGGCTTCTGTGAGTTCACC	
LaT06	56	W/Hot	1	0.3	F-	AGCCAGGCACATTAAGTGT	Archie, et al., 2003
					R-	TCTCCTAGAAAAGGTTACCACA	
LaT07	56	TD	2	0.7	F-	CCTGAGCCATTTTCTTGAG	Archie, et al., 2003
					R-	GATGGAGAGACAGATTTGCTAG	
LaT08	56	W/Hot	1	0.8	F-	ATGGACAGGCAGAAAGATTT	Archie, et al., 2003
					R-	TCCCAATAACAGGATAGCATT	
LaT13	56	W/Hot	1	0.8	F-	TGAGCTTCTGTAGGCTCTGA	Archie, et al., 2003
					R-	GCACTCGATAAACAGTGTTGA	
LaT16	56	TD	3	0.4	F-	TGGATGAATGGCAAATGG	Archie, et al., 2003
					R-	GCACAACACCTGCCTGTCA	
LaT24	56	TD	4	0.5	F-	AAGTTGAGAGATCAGCAAAGCA	Archie, et al., 2003
					R-	GATGTTCAGTCCTTCCTTAGCA	
LaT25	52	TD	3	0.5	F-	TGAGACCGTCTTCATGAGATG	Archie, et al., 2003
					R-	ATGCAAGCTTACAATGGCAG	

Dissertation Conclusions

In this dissertation I presented a comprehensive overview of the outcomes of an African elephant translocation. I provided information that should be useful to those planning future management actions, and I explored basic questions in animal behavior which are pertinent to studies of dispersing and migrating social species.

By examining the translocations' outcomes I showed that the first dry season of the translocated elephants in their new home was challenging. Upon release, some translocated elephants returned to the source site, the survival of the remaining translocated elephants was lower than that of the local population, they spent less time feeding and more time standing than the local residents, their body condition was poorer than that of the locals, and they associated with many conspecifics, only rarely interacting with unfamiliar locals.

By the end of the first year, the translocated elephants that remained at the release site seemed to have adjusted to their new home. Their behavior and stress hormones converged with those of the local population and they began to interact with fewer conspecifics, which included both familiar translocated elephants and local residents. Nonetheless, their body condition remained poorer than that of the local population and a few elephants continued to leave the release site in the months following the first dry season. These findings can be used to inform conservation practitioners about which animals should be targeted or avoided in future translocations, what time of year might be most or least suitable for such management actions, and what biological measures should be monitored carefully to ensure translocated elephants' welfare (e.g., body condition).

Furthermore, I made use of this translocation to address questions in the field of animal behavior. I found an interesting correlation between two behaviors, habitat exploration and approach distance to roads and human observers, suggesting that certain behavioral traits are linked. However, surprisingly, some attributes of animal settlement i.e., exploration and final distance from release site, are not necessarily tied to one another. Some of my findings suggest that behavioral changes over time and use of familiar habitat may buffer the effects of a novel environment on animals' physiology. I showed that social, non-territorial, animals interact with more conspecifics in a novel environment than they do when the environment is familiar, suggesting that there are added benefits to sociality in a novel environment. Finally, I showed that social animals form immigrant enclaves upon arrival at a new habitat, but that the social segregation between the newcomers and the local residents does not persist over time.

Throughout my work, conservation and basic science are intertwined, on the one hand, to provide recommendations for practitioners based on animal behavior research, and on the other hand, to enhance our knowledge of basic animal behavior by examining the outcomes of management actions. I hope my efforts to bridge the gap between conservation and animal behavior will be appreciated by individuals from both disciplines and that future studies will further implement this interdisciplinary approach.