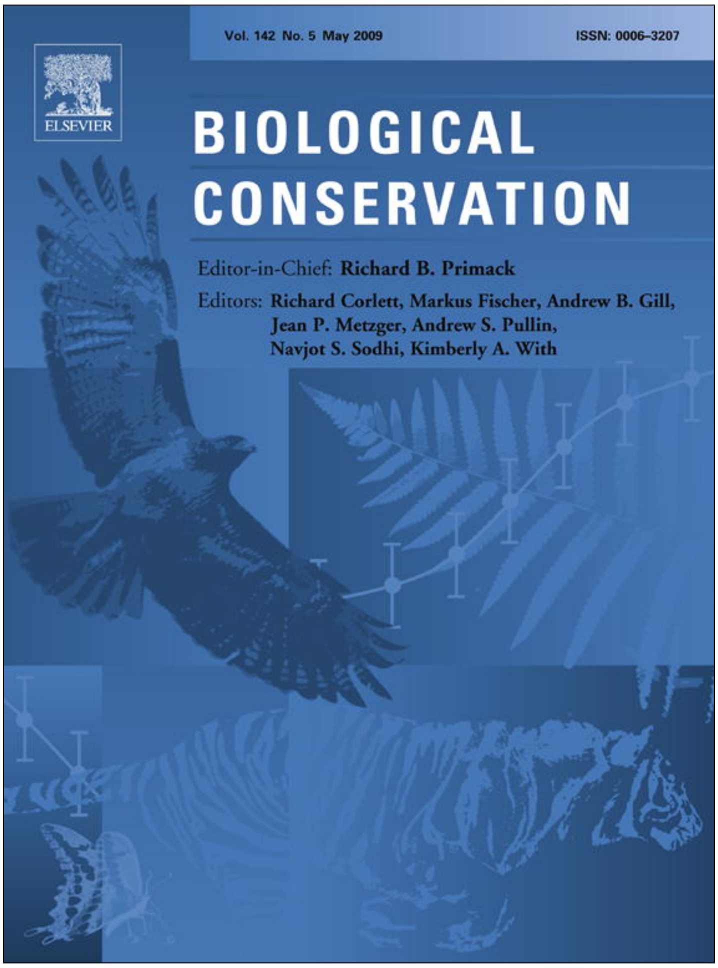
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Assessing translocation outcome: Comparing behavioral and physiological aspects of translocated and resident African elephants (*Loxodonta africana*)

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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 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 translocated animals' acclimation to their new home. Here we monitored the survival, physiology, and behavior of translocated African elephants (*Loxodonta africana*) and compared these measures to the local resident population at the release site. Adult male and female 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 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 behavioral time budgets of the translocated elephants converged with those of the local population over time. Finally, translocated elephants utilized habitat that was similar to their source site (hills and permanent rivers) more than did the local population. Based on these findings we recommend careful consideration of timing, release location, and individuals targeted in future elephant translocations. More broadly, we introduce and explore seldom used translocation assessment techniques.

1. Introduction

Relocating animals 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; Bar-David et al., 2005; Brightsmith 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), and Edgar et al. (2005)), for solving human-wildlife conflicts (Jones and Nealson, 2003; Wambwa et al., 2001), and for humanely reducing overpopulation at the source site (Garai and Carr, 2001). However, only 44% of translocations of endangered, threatened, or sensitive species have been successful (Griffith et al., 1989) and most translocations aimed at solving human–animal conflicts have failed (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.

Usually, 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; Reynolds et al., 2008). 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 provide information on whether they remain at the release site or leave it

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(Clarke and Schedvin, 1997; van Vuren et al., 1997; Cowan, 2001; Moehrenschlager and Macdonald, 2003; Sullivan et al., 2004; Stamps and Swaisgood, 2007; Pinter-Wollman, 2008, in press).

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 (Strum, 2005). However, it is not always possible to obtain pre-translocation data, 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 (Strum, 2005; 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 (Clarke and Schedvin, 1997; Tweed et al., 2003; 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, 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 the outcome of these massive management actions (for reports on male elephant translocations see Muir (2000), Garai and Carr (2001), and Slotow and van Dyk (2001)).

To assess the outcome of a translocation of 150 elephants conducted in Kenya in 2005, we 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 was examined to determine the short-term consequences of the translocation operation itself. Behavioral time budgets, habitat use, and physical measures, such as body condition and stress hormone levels, were compared between the translocated individuals and the local elephants. A convergence of these measures between the translocated and local elephants over time will indicate that the translocated elephants acclimated to their new home. A significant difference in these measures between the two populations will imply that the translocated elephants did not adjust to their new home in their first year. Movement patterns and social interactions of these translocated elephants are reported elsewhere (Pinter-Wollman, 2008, in press; Pinter-Wollman et al., 2009). This study is among the first to utilize both behavioral and physiological measures for assessing the outcome of a translocation of a long-lived animal (see also Strum (2005)). In addition, our 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, we present here novel assessment methods that we believe will be vital for many future studies on the outcomes of conservation actions.

2. Methods

2.1. 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 (4–4.3°S and 39.5–39.3°E) to Tsavo East National Park (2.00–3.70°S and 38.13–39.30°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 the 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 300 mm to 700 mm (van Wijngaarden, 1985), while Shimba Hills is part of the coastal plateau with an average annual rainfall of 1500 mm and a humid equatorial climate (Kahumbu, 2002). 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) (van Wijngaarden, 1985) whereas the source site, Shimba Hills is a small (250 km^2) reserve surrounded by human settlements (Kahumbu, 2002). The two Tsavo National Parks (East and West) are home to the largest elephant population in Kenya (approximately 9000 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).

2.2. 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 (see also Muir (2000)). 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 (Sitrack, New Zealand) to enable detailed post-release tracking of movement patterns.

The locations of translocated and local Tsavo elephants were recorded for 1 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 locations 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.

2.3. Survival

Post-translocation monitoring and reports from KWS rangers, and from the long-term Tsavo elephant researcher (Dr. Barbara McKnight) 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 (suckling or in very tight association), but were then missing when their mother was sighted again, and did not reappear, were defined as 'probably dead calves' (Moss, 2001). 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.

We 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, we 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).

2.4. 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), and close enough to the observer (approximately 50 m), 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 and 2 based on the criteria described in Table 1 (A–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 (McKnight, 2000). 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).

2.5. Hormone collection and analysis

When possible, fresh 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 50 cc 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 1 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)). All hormone analyses were carried out by Rebecca Nelson Booth at Samuel Wasser's Lab in the Department of Biology, University of Washington.

2.6. Behavioral time budgets

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 from a river or water hole;

Table 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.

Age class	Calves		Juveniles		Adults		Total
Sex	Males	Females	Males	Females	Males	Females	
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*

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.

2.7. 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 based on van Wijngaarden (1985) and 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 100 m 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.

2.8. 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 Fig. 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 (Fig. 1).

2.9. 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 was 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

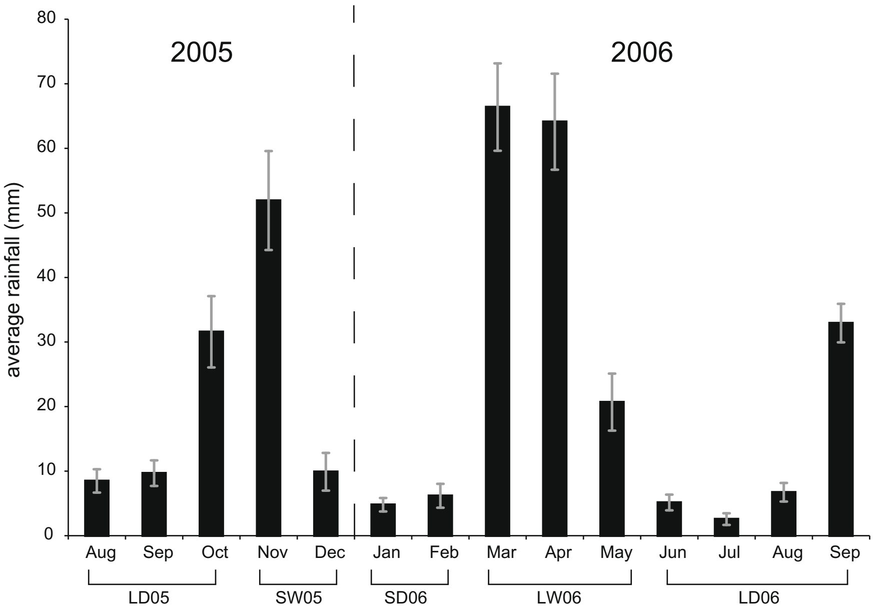

Fig. 1. Rainfall and seasons in Tsavo East National Park: Average (±SE) rainfall (mm) obtained from 22 to 26 rain gauges distributed throughout Tsavo East National Park, by month, during the years 2005 (left of the dashed line) and 2006 (right of the dashed line), for the period during which this study 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.

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 behavioral time budgets and habitat use of translocated and local elephants were examined using a Chi square test. The estimated probability distributions for the behaviors stated above (foraging, standing, and walking) or habitats used 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).

3. 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 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 1). The fate of 41 (27%) of the translocated elephants was unknown. Twenty four of the translocated elephants died (16% of the 150 elephants, or 22% of the 109 translocated elephants whose fate is known). 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 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: $P = 0.0009$).

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 6 months after release when the calf's age was estimated to be 1 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.

3.1. 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). 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, Fig. 2). The only seasonal

Table 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 was 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.

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**

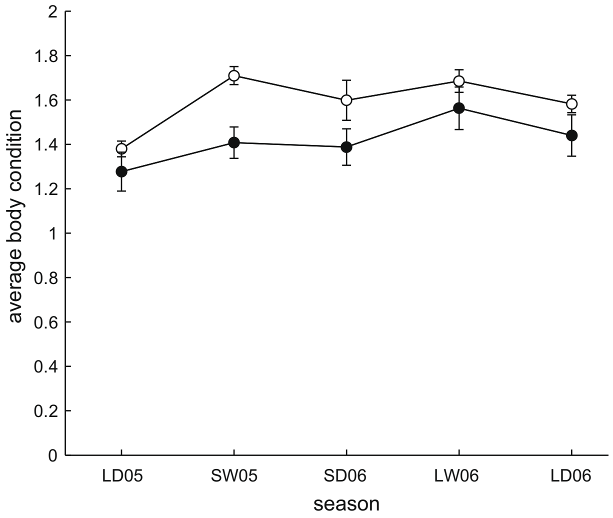

Fig. 2. Translocated and resident elephants' body condition over time: Average (±SE) body condition of adult translocated elephants (black circles) and local Tsavo elephants (white circles) throughout the study period, by season. Body condition ranges from 0 (poor) to 2 (good) based on Wemmer et al. (2006). 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).

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) with body condition improving after LD05. Females had a significantly poorer body condition than males ($P < 0.001$, Table 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 (McKnight, 2000) and elephants' gestation period is 22 months whereas the duration of this study was 1 year.

3.2. 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 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, sex, and storage duration in ethanol were not significant effects in the model (Table 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 (nanograms hormone per gram sample) 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 6.5 ng/g could have been detected at a power of 0.82 or higher and at alpha = 0.05.

3.3. Behavioral time budgets

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; $P = 0.012$, $X^2 = 8.84$, $N = 246$, Fig. 3). 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: $P = 0.51$, $X^2 = 1.33$, $N = 239$; SD06: $P = 0.68$, $X^2 = 0.75$, $N = 199$; LW06: $P = 0.22$, $X^2 = 3.03$, $N = 183$; and LD06: $P = 0.63$, $X^2 = 0.92$, $N = 531$, Fig. 3). Thus, over time the translocated elephants' behavioral time budgets converged with those of the local population.

3.4. 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: $P < 0.0001$, $X^2 = 116.67$, $N = 941$; SW05: $P < 0.0001$, $X^2 = 49.54$, $N = 402$; SD06: $P = 0.008$, $X^2 = 15.59$, $N = 415$; LW06: $P < 0.0001$, $X^2 = 26.94$, $N = 313$; LD06: $P < 0.0001$, $X^2 = 67.18$, $N = 866$, Fig. 4). 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

Table 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 was significant and therefore they were not included in the final model.

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

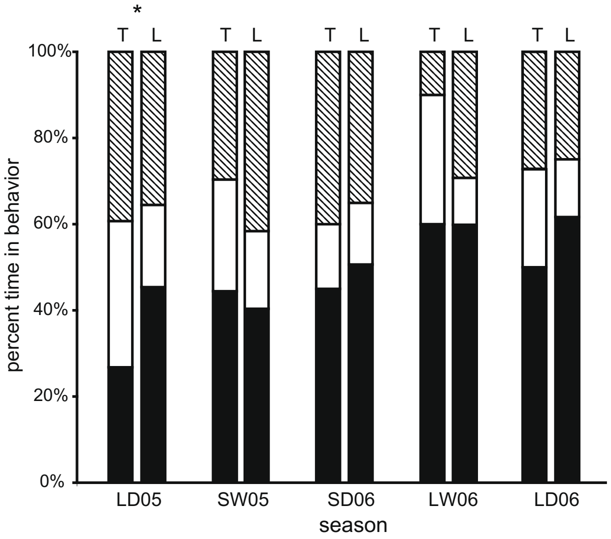

Fig. 3. Translocated and resident elephants' behavioral time budgets over time: Percent observations during which translocated elephants (T) and local elephants (L) were seen foraging (black), standing (white), or walking (hatched) throughout the study period, by season. Season notation as follows: LD05 – 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. An asterisk denotes statistically significant ($P < 0.05$) time budget differences between translocated and local elephants.

did the local elephants, but no difference was observed between the time spent by locals or translocated elephants in the bush-grass habitat (Fig. 4). Thus, the translocated elephants' habitat use was different from the local elephants' habitat use, and did not change over time.

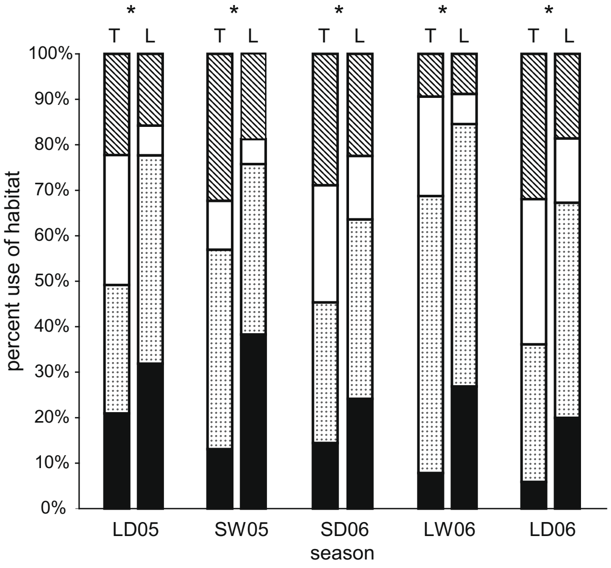

Fig. 4. Translocated and resident elephants' habitat use over time: Percent observations during which translocated elephants (T) and local elephants (L) were seen in the different habitats: hills (white), permanent rivers (hatched), bush (black), or bush-grass (dotted) throughout the study period, by 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. An asterisk denotes statistically significant differences ($P < 0.01$) in habitat use between translocated and local elephants.

4. Discussion

Mortality rate of adult translocated elephants was significantly higher than that of the local Tsavo population. All translocated elephant deaths occurred within 2 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 Pinter-Wollman (2008, in press)). 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. It is possible, although less likely, that the observed poor condition of the translocated females' mammary glands resulted from calf poaching or predation because calves are not poaching targets due to their small tusks, and because predation by lions is very rare in elephants (Loveridge et al., 2006).

The physiological measures we assessed provided conflicting results. The body condition of the translocated elephants was significantly poorer than that of the local elephants throughout all seasons of the study. This finding supports the idea that arriving at a novel environment may have negative effects on newcomers (e.g., because of being unfamiliar with appropriate food resources or due to competition with locals). It is possible that the starting body condition of the translocated elephants was poorer than that of the local Tsavo residents. Although pre-translocation data are unavailable, we believe this alternative is unlikely because Shimba Hills was lush and green before and at the time of the translocation whereas Tsavo East was in the midst of a long dry season with little available forage. 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 because 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 behavioral time budgets 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 because 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 (Pinter-Wollman et al., 2009). 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 (Pinter-Wollman et al., 2009) 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 behavioral time budget 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 contain habitat similar to the source site and 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, 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, we 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. We 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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