Hunting performance of captive-born South China tigers (*Panthera tigris amoyensis*) on free-ranging prey and implications for their reintroduction

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Abstract

The South China tiger (*Panthera tigris amoyensis*), although listed by the IUCN as critically endangered, is probably extinct in the wild. This leaves captive-born animals as the only stock available for reintroductions. Because reintroduced animals will not survive in the wild unless they hunt proficiently, we aimed to determine whether captive-born tigers were able to hunt free-ranging prey and to evaluate their hunting performance as a criterion for reintroduction. The effect of other variables on subsequent hunting success, such as the availability of stalking cover and the upbringing history of tigers while they were cubs, were also explored given their relevance in reintroduction programmes. Twelve tigers over two years of age were fitted with GPS collars and placed individually in 100ha enclosures to determine their kill rate of blesbuck (*Damaliscus pygargus*), as a measure of their hunting performance. All tigers but one successfully hunted blesbuck, although kill rate varied substantially amongst individuals, ranging from one blesbuck every 3.14 days to no blesbuck. Tigers also killed other species, indicating plasticity in their hunting behavior, and showed higher kill rates in the enclosure where cover was more abundant, confirming the importance of stalking cover in hunting success for this species. Results showed that the presence of the mother during cub development was not necessary for cubs to hunt later in life, although it had a positive effect on kill rate. Our study represents the first empirical evidence that captive-born tigers can successfully hunt free-ranging prey adequately to meet their energetic demands, validating the use captive animals to recover wild populations, should other reintroduction criteria be met. Moreover, that tigers adapted to the African veld ecoregion suggests they should be able to adapt back to southern China where opportunities for stalk and ambush are more numerous.

Key words: South China tiger; captive-born; hunting behavior; reintroduction; stalking cover; kill rate.

1. Introduction

The South China tiger is the most endangered tiger subspecies (Chundawat et al., 2011; Tilson et al 2010). Due to habitat loss and fragmentation, tiger eradication campaigns, uncontrolled hunting, and human encroachment into tiger habitat the South China tiger suffered major population declines during the last century (Chundawat et al., 2011; Tilson et al., 2004). Listed as Critically Endangered by the IUCN (Nyhus, 2008), it has not been directly observed in its habitat since 1970, suggesting it is possibly extinct in the wild (Chundawat et al., 2011, Tilson et al., 2004). Restoration of wild populations within the subspecies' historical range will therefore require reintroduction efforts (Driscoll et al., 2012; Tilson et al., 2010).

The IUCN indicates that reintroduced animals can be either from a captive or wild source (IUCN, 2013). However, the use of wild-caught individuals is generally preferred (Breitenmoser et al., 2001; Christie, 2009; Jule et al., 2008), as reintroductions using captive animals are less likely to be successful (Fischer and Lindenmayer, 2000; Griffith et al., 1989; Jule et al., 2008; Mathews et al., 2005; Wolf et al., 1996). Nonetheless, for the South China tiger – as for an increasing number of other taxa (Jule et al., 2008; Macdonald, 2009; Wilson and Stanley Price, 1994) – the only animals available for reintroduction are from captivity (Tilson et al., 2004; Tilson et al., 2010).

When animals are in captivity for generations their behavior may experience artificial selection to adapt to their captive environment (McPhee, 2004; Sutherland, 1998). These adaptations, although beneficial to captivity can compromise their survival in the wild (Biggins et al., 1999; Kleiman, 1989; Jule et al., 2008), where deficiencies can be seen in foraging/hunting, social interactions, breeding and nesting, or locomotory skills (e.g. Snyder et al., 1996; Vickery and Mason, 2003; Wallace, 2000). However, these animals can be behaviorally conditioned to develop those skills that might have been lost during captivity (IUCN, 2013). In fact, pre-release conditioning has modified behaviors in several mammal species in ways assumed to be beneficial to survival (e.g., Kleiman et al., 1986; Phillips, 1990; Soderquist and Serena, 1994; Stanley-Price, 1989; Vargas and Anderson 1999).

Save China's Tigers is a charity that in collaboration with the Chinese State Forestry Administration (SFA) breeds and prepares captive-born South China tigers for reintroduction to restored protected areas within the subspecies' historic range in China (Nyhus, 2008; Tilson et al., 2010). With the support of SFA, in 2003 and 2004 the charity relocated four South China tiger cubs from Chinese zoos to Laohu Valley Reserve (LVR), a private captive facility in South Africa (Breitenmoser et al., 2006, Tilson et al., 2010). South Africa was chosen to establish the breeding facility as land, free-ranging prey, and wildlife expertise were available. At LVR tigers are provided opportunities under semi-wild conditions to acquire hunting and other survival skills to prepare them for reintroduction in China. Despite concerns relating to the ex situ nature of the project by some in the conservation community (Anon, 2003, Tilson et al., 2010), SFA recognized the project as the first practical step towards the restoration of South China tigers to the wild (Tilson et al., 2010), and considered it consistent with IUCN guidelines for reintroductions as China lacked the necessary habitat, expertise and infrastructure to conduct the project in situ. Recently, Chinese authorities and international organizations have identified existing protected areas of sufficient size within the subspecies' historic range as potential sites that could be suitable for reintroduction subject to habitat restoration (Qin et al., 2015; State Forestry Administration of China, 2010; Tilson et al., 2010).

The success of any carnivore reintroduction will depend, among other biological and socio-economic considerations, on each animal's ability to secure prey efficiently (Christie, 2009; Rabin, 2003; Vargas and Anderson 1999). If tigers at LVR are to be returned to the wild, an objective measure of their hunting performance is necessary. The goals of this study were firstly, to determine whether captive-born tigers were able to successfully hunt free-ranging prey and secondly, to evaluate their hunting performance as a criterion to select candidates for reintroduction. Our third goal was to investigate the importance of stalking cover in tiger hunting success due to its relevance for the selection of candidate sites for reintroduction. Finally, because its importance on pre-release training programmes, we explored the effect of upbringing history on hunting performance later in life. In domestic cats (*Felis catus*), the presence of the mother during exposure to prey in infancy improves subsequent hunting behavior (Caro, 1980).

Although rehabilitation programmes have been conducted with *P.t. tigris* (Ramesh et al., 2011) and *P.t. altaica* (Miquelle et al., 2001), two important factors differentiate them from the present study. Firstly, these efforts dealt with orphaned cubs and not captive-born tigers, and secondly, they were conducted within tiger distribution range. To the best of our knowledge, the present study is the first to report and assess hunting performance in semi-wild conditions for captive-born tigers.

2. Methods

2.1 Study area

The study was conducted at Laohu Valley Reserve (LVR), in the Free State Province (South Africa). LVR lies within the Acocks Veld Type 36 or False Upper Karoo (Acocks, 1975). Elevation ranges from 1 200 m to 1 479 m and landscape consists of gently to moderately sloping valleys and hills. Grasslands occur on the lower-lying flat areas, with karroid shrubs on the rocky hill slopes (Viljoen, 2014). Fairly dense stands of shrubs and trees occur along rivers and in ravines. Mean annual rainfall is 400 mm (Milton and Dean, 1995), where about 60% of the annual rainfall occurs in the form of thunderstorms during January-April. Summer days are hot but frost is common during winter, with occasional snowfall.

LVR is approximately 33 000 ha with tigers confined to predator-proof fenced enclosures ranging from 0.4 ha to 100 ha. Enclosures have natural environmental features and substrate, and free flowing fresh water. They are delimited with solar powered electric wire fencing that complies with the National Norms and Standards for predators in South Africa (Botha, 2005). Two 100 ha enclosures, named as Camp A and Camp B were used to test hunting performance and the importance of stalking cover in hunting success. These enclosures were contiguous to each other and therefore plant community and geomorphology were similar, with open habitat and denser vegetation along streams. However, the amount and distribution of shrubs, as well the extension of contiguous open areas was different between the two enclosures (Figure 1). Camp A had more shrubs and less continuous open areas, while in Camp B shrubs were less numerous and the predominant landscape feature was open areas devoid of any shrubs.

2.2 Study tigers

Seven male and five female South China tigers were identified for study. Tigers were over 20 months old to ensure that canine replacement was complete as these teeth are believed to be essential for killing prey. Complete canine replacement occurs around 18 months of age (Smith, 1993).

All tigers were captive-born, either at LVR or at zoos in China and subsequently transported to LVR as young cubs (Tilson et al., 2010). Zoo-born cubs were exposed to potential hunting opportunities with conspecifics, as a mother figure was not an option. Cubs born at LVR were kept with their mothers and exposed to prey until the age of 5, 13 or 15 months, and then separated from their mothers but kept with siblings or other cubs of similar age. In two occasions when a mother rejected her singleton, the cub was hand-reared until rejoining its mother and/or siblings at the age of nine months.

2.3 Tiger prey

The hunting enclosures were stocked with free-ranging blesbuck (*Damaliscus pygargus*) at the beginning of each testing period. We chose blesbuck over other species as their body mass is relatively close to that of sika deer, *Cervus nippon* (67kg, Whitaker and Hamilton, 1998). Sika deer are farmed in China (Harris, 2008) and an option to augment their depauperate populations in potential reintroduction sites (Jiang and Li, 2009; Qin et al., 2015; Tilson et al., 2008). Also, blesbuck are readily available and affordable in South Africa, well adapted to this habitat (Lloyd and David, 2008) and unlike other African ungulates, adapt well to fenced enclosures. Stocking the enclosures with warthog (*Phacochoerus africanus*) or bush pig (*Potamochoerus larvatus*) as African surrogates for wild boar (*Sus scrofa*), one of the tiger's most preferred species (Hayward et al., 2012; Sunquist and Sunquist, 2002) was discarded as they are difficult to contain by fences. On the other hand, Sambar (*Rusa unicolor*) although also preferred by tigers (Hayward et al., 2012) is rare in China (Tilson et al., 2004) and therefore unlikely to be in the diet of tigers unless introduced in the area prior tiger reintroduction.

Blesbuck density in the hunting camps ranged from 32 to 42 animals/km^2 to provide similar hunting opportunities to all tigers, although previous observations indicate that in these camps hunting success is not related to blesbuck density when below 60 blesbuck/km^2 (Fàbregas et al., 2012). Blesbuck were sourced either from LVR or surrounding game farms. Because the size of the enclosures and the natural features within, both predator and prey were "free-ranging" with regards to hunting. The variety of features on the landscape offered tigers with a variety of choices for stalking and ambushing. Similarly, prey could execute evasive behaviors to avoid predation by choosing parts of the enclosure that minimized predation risk, such as open areas. Blesbuck ewes lambed every year indicating that the hunting enclosures were of adequate size and provided adequate safety and forage to meet their survival and reproductive needs. Enclosures were re-stocked between testing periods, when tigers had been removed. New blesbuck used for restocking were allowed at least 48 h to join the resident predator-aware herd and become acquainted with the terrain before a tiger was introduced. Aside of blesbuck, other naturally occurring species such as Chacma baboon (*Papio ursinus*), aardwolf (*Proteles cristata*), and steenbuck (*Raphicerus campestris*) frequented the enclosures from time to time.

2.4 Design

Depending on husbandry constraints (e.g., ungulate re-stocking schedules) each tiger spent 20 to 31 days in each enclosure to test their hunting performance. To track hunting activity in the enclosure and ensure tiger welfare, blesbuck were counted daily from outside each enclosure with a spotting scope and/or binoculars, and tiger condition was visually monitored whenever a tiger approached the perimeter fence. When a tiger had not killed blesbuck for six days and started to show indicators of poor body condition (i.e., visible skeleton along spine, hipbones and ribs, coarse and spikey coat, general display of weakness, nictitating membrane covering part of the eye), a small portion (i.e., 6-8 kg) was thrown over the enclosure fence in a location where the tiger could not see, in order to prevent the tiger to associate food with humans and mimic scavenging behavior. If two days after supplementary feeding the tiger had not hunted and lost further condition, a larger piece (i.e., 15-25 kg) was fed following the same protocol to allow recovery, as tigers that lose substantial body condition often seem too weak to hunt effectively (Viljoen, personal communication), preventing weight gain and condition recovery. Data were collected during three periods: October to November 2012, April through November 2013, and March through June 2014. We did not collect data from November through March as this is lambing period for the blesbuck and we elected to not expose the more vulnerable prey and their lambs to the stress of being hunted.

Hunting performance was expressed as average numbers of days per blesbuck kill for each tiger and enclosure. The higher the number of days between blesbuck kills, the lower the kill rate. To identify and count feeding sites, tigers were fitted with GPS remote drop-off collars (Vectronics, Germany) by immobilizing them with a combination of medetomidine (50-100 µg/kg) and ketamine (1-2 mg/kg) administered intramuscularly by means of a CO_2-propelled darts.

GPS data were used to detect spatial and temporal clustered locations that could indicate a potential feeding site (Anderson and Lindzey, 2003). Spatial error was estimated in each of the habitat types where GPS clusters were generated (i.e. riparian, under bush, dry ravine and open area). Mean error was 4.49 m in one collar (minimum = 0.37 m, maximum = 23.24), and 4.31 m for the other collar (minimum = 0.28, maximum = 26.83 m). Collars were programmed to record location at 15 minute intervals (144 readings/tiger/day) to maximize opportunities of identifying small prey feeding locations (Webb et al., 2008). GPS data were downloaded and imported into ArcGIS v.10.2 (ESRI, Redlands, CA, USA) to identify GPS location clusters. To account for GPS collar error and to maximize the chance of finding small prey feeding locations, we considered any group of more than eight consecutive GPS points (i.e. ≥ 2 h) and within 25 m of each other as a cluster to be searched as a potential feeding site. Clusters were uploaded into a hand-held GPS device (Garmin e-Trex 30, International, Olathe, KS, USA) and used to search for carcass remains or other evidence of a kill (i.e., prey digesta, plucked hair, bone, horns, hide). All clusters were visited the day after the tiger was removed from the enclosure at the end of its study period with a maximum of 33 days between the occurrence of a cluster and its visit. This search schedule avoided displacing tigers from kills and was adequate to prevent losing information to carcass decomposition or scavenging since caracals (*Caracal caracal*), black backed jackals (*Canis mesomelas*), and small scavengers such as members of the Herpestidae family were also present in the camps (Miller et al., 2013; Sand et al., 2008; Webb et al., 2008). Prey remains were photographed and, if unconfirmed in the field, representative material was collected for identification at the Centre of Wildlife Management, University of Pretoria (South Africa).

This research study was carried out under an agreement signed between the Chinese State Forestry Administration and Save China's Tigers, and was approved by the University of Pretoria Animal Use and Care Committee (protocol V053-12).

2.5 Data analysis

Five categorical variables were analyzed to explore their relationship with hunting performance (Table 1). Differences in blesbuck kill rate were compared among categorical predictors using Mann-Whitney U and Kruskal-Wallis tests. Kill rates between camps A and B were compared using Wilcoxon signed-rank tests. We tested a multivariable regression with five variables, but we were unable to generate a model, most likely due to small sample size (n= 12 tigers). Because of this we used non-parametric tests. The effect of upbringing history as well as presence of the mother on subsequent hunting performance were treated as descriptive data. Statistical analyses were performed using SPSS Version 22 (International Business Machines Corp., Armonk, NY, USA) and significance was set at 0.05.

3. Results

We identified 834 GPS clusters; 428 in Camp A and 406 in Camp B. All cluster locations were visited and we found prey remains at 96 sites (i.e., feeding sites) belonging to 69 presumed kills, 50 of them blesbuck.

All tigers were able to successfully hunt free-ranging prey, and all but one were able to kill blesbuck. Hunting performance however varied substantially among individuals (Table 2). Among males, T1 had the highest kill rate in Camp A (3.14 days/blesbuck kill), but killed no blesbuck in Camp B. His male sibling T6 had the highest kill rate in Camp B (4.86 days/blesbuck kill). Lowest kill rate corresponded to T12, for whom we did not identify any blesbuck remains in either enclosure although he did kill a leopard tortoise (*Stygmochelys* *pardalis*) and a steenbuck in Camp B. He was removed from Camp A after 10 days due to rapid loss in body condition. Amongst females, T2 had the highest kill rate in Camp A with a blesbuck kill every 4.86 days plus two baboons and a Cape porcupine (*Hystrix africaeaustralis*). Her female sibling T3 had a similar kill rate in Camp A (5 days/blesbuck kill), and second highest blesbuck kill rate in Camp B. The lowest kill rate amongst females corresponded to T9 who killed one blesbuck every 10.5 days on average while in Camp A, and just one blesbuck while in Camp B. None of the tigers but T8 had to be fed while in Camp A, but in Camp B seven tigers received supplementary feeding.

Blesbuck kill rate did not differ significantly between sexes ($p= 0.343$) or age categories ($p= 0.469$), although older adults showed lower kill rates than other age groups. Zoo-born tigers had the lowest kill rate but they were also the oldest individuals, making it difficult to determine whether their kill rate was due to age or lack of the mother during development.

As expected, hunting performance differed between camps ($p= 0.008$), being higher in the enclosure with more stalking cover (Camp A mean: 0.14 ± 0.05 blesbuck kills/day, Camp B mean: 0.04 ± 0.04 blesbuck kills/day) (Figure 2). Aside from blesbuck, tigers killed seven other species while in the hunting camps, including mammals (aardvark, *Orycteropus afer*, steenbuck, Cape porcupine, Chacma baboon, aardwolf, Cape hare, *Lepus capensis*), one bird (Hadada ibis, *Bostrychia hagedash*), and a reptile (leopard tortoise). The number of species killed in Camp B was more than double than that in Camp A (Camp A= 3 species, Camp B= 8 species) despite the fact that kill numbers in Camp B were less than half than those in Camp B. However, the number of species killed by each tiger was not significantly different between camps ($p= 0.224$).

No statistical analyses were performed to assess the relationship between the variables "effect of the mother during cub development" and "upbringing history" on hunting performance due to small sample size within categories. Exploratory analysis for those two variables indicated that tigers that were raised by their mothers as cubs while exposed to prey showed higher kill rates than those who were not, although data overlap was substantial between groups (Figure 3). Regarding the upbringing history, cubs who were separated from their mothers at an earlier age had the highest kill rates, but data were also highly dispersed for this group (Figure 4). Tigers that were hand-reared and then rejoined with their mothers or siblings killed blesbuck in both camps, ranking second highest on measures of hunting performance.

4. Discussion

4.1 Hunting in captive-born tigers

Our data demonstrate that tigers that have been in zoo conditions for generations as well as their offspring are able to successfully hunt free-ranging prey provided that they are housed in large naturalistic enclosures, exposed to free-ranging prey, and have minimal human intervention. These results challenge the idea that only wild tigers can teach their young to hunt (Fraser, 2009). Christie and Seidensticker (1999) hypothesized that captive-bred tigers should be able to hunt successfully arguing that basic hunting behavior is essentially instinctive, and reporting that captive-born mountain lions (*Puma concolor*) were able to kill large prey within a few days after release (Belden and McCown, 1995). The present study represents the first empirical evidence that captive-born tigers can learn to hunt successfully. Given that one of the causes of death in introduced captive carnivores is starvation (Jule et al., 2008), these results have important implications not just for tiger conservation, but also for restoring populations of other large carnivore species.

4.2 Hunting performance as a criterion for reintroduction

All tigers over two years old were able to hunt free-ranging prey, but hunting performance (i.e. kill rate) varied greatly amongst individuals. These differences highlight the need to consider individual hunting performance, and not just the ability to hunt as one of the criteria to select candidates for reintroduction. That a tiger manages to make one kill does not necessarily imply that it can hunt with the necessary frequency as to sustain itself and reproduce. In many reintroduction programmes, selection of release candidates is based solely on fulfilment of age, sex and health criteria (Sarrazin and Legendre, 2000; Yalden, 1993). However, consideration for selection should also include behavioral skills such as food acquisition (International Academy of Animal Welfare Sciences, 1992; Kleiman, 1989), as well as behavioral traits (e.g. boldness, Bremner-Harrison et al., 2004). Amongst the criteria that reintroduction candidates will certainly have to meet before release (e.g., Box, 1991; Kleiman, 1989), it is necessary to ensure that candidates can successfully hunt as to meet their energetic demands in the new environment to increase their chances of survival (Christie, 2009; Macdonald, 2009; Rabin, 2003; Vargas and Anderson, 1999), and their ability to reproduce (Seidensticker, 1976; Sunquist 1981; Sunquist et al., 1999).

Several field studies have estimated tiger energetic requirements based on kill rates. For instance, Miller and colleagues (2013) reported kill rates between 5.89 and 7.18 days/kill for Amur tigers in the Russian Far East. Seidensticker (1976) estimated that in Nepal (Chitwan N.P.), Bengal tigers killed once every 5 to 5.98 days, while Sunquist (1981) reported kill rates in the range of 7.30 to 9.13 days/kill for the same subspecies in the same area. Although energetic requirements depend on many factors such as climatic conditions (Mautz and Pekins, 1989) or reproductive stage (Sunquist et al., 1999, Miller et al., 2014), it seems reasonable to predict that any tiger unable to kill a medium-size ungulate (60-70 kg) every 7-8 days will not survive. From an animal welfare point of view, the release of wild animals with poor chances of survival would not only compromise their wellbeing (Christie, 2009) but may also be illegal in some countries (e.g., United Kingdom: Abandonment of Animals Act, 1960). Therefore we strongly advocate that hunting proficiency is evaluated prior release of any carnivore (Christie, 2009; IUCN, 2013).

4.3 Effect of upbringing history on hunting performance

Our study sample, although quite large compared to other tiger studies (e.g., in captivity: Bashaw et al., 2007; Seal et al., 1985; in the wild: e.g., Miller et al., 2013; Seidensticker, 1976; Sunquist, 1981), was too small to allow statistical analyses of the effect of upbringing history on hunting performance. However, given its relevance for pre-release training programmes, and considering that it has never been explored in wild or captive tigers we regard our results to be useful. The fact that all tigers were able to kill prey, regardless of whether or not they were raised by their mothers indicates that, as in the case of domestic cats (Leyhausen, 1979), the presence of the mother while exposed to prey during infancy is not *necessary* for cubs to hunt successfully later in life. However, cubs raised by their mothers showed higher kill rates, suggesting a facilitating role of the mother on the development of subsequent hunting behavior (in cats: Caro, 1980). In several wild felid species such as tigers, lions, leopards or cheetahs, older cubs accompany their mothers during hunts before they start hunting on their own (Caro, 1987; Kitchener, 1999; Schaller, 1967; Skinner and Smithers, 1990; Turnbull-Kemp, 1967). This behavior suggests that mothers may be offering their offspring opportunities to learn for themselves during these hunting expeditions (i.e., opportunity teaching, Caro and Hauser, 1992), as opposed to actually teaching them to hunt (Ewer, 1969; Leyhausen, 1979).

The period of time before independence is much longer for larger than smaller felids (Kitchener, 1999). For tigers, this period lasts until the next litter starts moving along with the mother, at 19-28 months (Smith, 1993). Aside from a longer development period required for the permanent dentition to develop (Leyhausen, 1979; Smith 1993), it has been suggested that offspring of larger species need an extended opportunity to learn since they have to deal with larger, more difficult and potentially injurious prey (Kitchener, 1999). According to this line of reasoning, tigers that stayed longer with their mothers (i.e., 13-15 months in our sample) should be better hunters. Interestingly, our results showed otherwise: those tigers that were separated earlier from their mothers or were hand-reared ranked first and second highest kill rates, respectively. Our results should be treated with caution as sample size was limited and data overlapped greatly with other upbringing regimes, but further research on this topic would help to understand the role of the mother in the development of hunting skills in cubs for this species.

For domestic cats social experience per se is not necessary for the development of the prey killing response (Kuo, 1930). However, Caro (1981) demonstrated that siblings played a role in prey capture skills of other kittens by focusing attention on and motivating interactions with prey. All tigers at LVR were raised with another tiger (i.e., mother and/or related or unrelated cub), so we lack a control group to test whether social upbringing promotes efficient hunting in tigers, or if it is at all necessary for the development of hunting skills. But because of the similarity of prey capture behaviors amongst felids (Kitchener, 1999) it seems reasonable to assume that young tigers would benefit from being raised with conspecifics rather than alone. Based on previous findings and our results, it is therefore recommended that candidates for reintroduction are kept with their mothers while exposed to prey. In those cases where the mother is not available (e.g., orphaned cubs, translocation of the offspring without the mother), cubs should be kept with conspecifics.

4.4 Stalking cover, behavioral flexibility and implications for tiger reintroduction

As stalk and ambush predators (Schaller, 1967; Sunquist, 1981), tigers rely on concealment to pursue prey. Sunarto and colleagues (2012) reported that Sumatran tigers (*P.t. sumatrae*) preferred areas with abundant understory cover, while Karanth and Sunquist (2000) found that tigers made most of their kills (81%) in dense to moderate cover. The significantly lower kill rate in the enclosure where stalking cover was scarce (Camp B) is consistent with previous studies where cover has been found to be important for successful hunting, highlighting the need of considering this feature when identifying candidate sites for reintroductions.

Tigers show considerable flexibility in predatory behavior, changing their hunting patterns and tactics to kill prey species that vary greatly in size (Seidensticker and McDougal, 1993; Sunquist et al., 1999). Tigers at LVR also showed high plasticity on their hunting behavior by taking several species other than blesbuck. While kills in Camp A doubled those in Camp B, the number of species killed in Camp B was more than double than in Camp A. The scarcity of stalking cover for tigers in Camp B could be responsible for this outcome, as lack of cover makes blesbuck less vulnerable to predation (Elliot et al., 1977; Schaller, 1967) forcing tigers to hunt smaller prey items. This also occurs in the wild, where tigers hunt smaller species when preferred ones are unavailable or at very low densities (Biswas and Sankar, 2002; Karanth and Sunquist, 1995; Seidensticker and McDougal, 1993; Sunquist, 1981).

Tigers are highly adaptable species with the ability to live in a diversity of habitat types and tolerate a wide range of temperature and rainfall regimes (Miquelle et al., 1996; Sunquist et al., 1999; Wilting et al., 2015). Our results show that this ability applies even beyond their distribution range. However, there are concerns about whether tigers at LVR, now adapted to hunt African prey in African landscapes will be able to prey on Chinese species in southern China. The South China tiger is historically adapted to subtropical evergreen and deciduous mixed forests (Houhe, 2004; Hupingshan, 2004) and yet has been able to cope in the African *veld*. Tiger cubs which arrived to LVR from Chinese zoos learned to kill prey species that neither they nor their ancestors had previous exposure to. Based on these facts, we consider that there is no reason, a priori, to believe that LVR tigers will not be able to adapt again to their former range in China where in fact, opportunities for concealment (and therefore effective hunting) are greater than in South Africa. Overall, our results support the possibility of establishing ex situ pre-release training programmes for tigers and maybe for other carnivores as well when doing it in situ is not an option. In these cases, a soft release strategy is highly recommended so reintroduced animals have the opportunity to adapt to the environmental conditions and prey species of their historic distribution range while still under human control and in a safe environment (i.e. captivity). Likewise, disease and parasite transmission (Cunningham, 1996) should be properly addressed, given that when conservation projects are located outside the species distribution range these risks are higher than for in-situ conservation programmes (IUCN, 2013).

5. Conclusions

Our study results demonstrate that tigers that have been in zoo conditions for generations can successfully hunt free-ranging prey when under the right housing/management conditions, showing behavioral plasticity in their hunting behavior. For the South China tiger, where captive animals are the only possibility for reintroduction, these results bring hope for the restoration of the subspecies in the wild. Based on the differences observed in kill rate amongst studied tigers, we highly recommend to consider hunting performance as one of the criteria to select candidates for reintroduction. Likewise, areas with stalking cover should be favored when selecting candidate reintroduction sites as cover has proved to play a crucial role in tiger hunting success.

Our data suggest that the presence of the mother while exposed to prey during cub development is not necessary for tigers to hunt later in life, although it has a positive effect on kill rate. We could not make solid statements about the effect of age or upbringing history on subsequent hunting performance due to our sample size. Also, no tiger was raised in isolation and all of them were exposed to hunting opportunities before the study started. This situation makes it impossible to answer questions such as what is the period of training required before a tiger can make a successful kill, or whether tigers can learn to hunt if isolated from conspecifics. Further research on these and other variables that might be related to the acquisition of hunting skills by cubs would be very helpful in designing and improving pre-release training and rehabilitation programmes for tigers and maybe other carnivores.

The South China tiger seems to have adapted to South Africa, suggesting that the reverse process (i.e., adapting back to China) could also be possible. This presents the possibility of stablishing ex situ pre-release training programmes when needed, increasing the possibilities in the conservation toolbox to restore this and maybe other endangered carnivores. However, a soft release strategy as well as a thorough evaluation of the risks associated with the transportation of animals from areas outside the species distribution range are highly encouraged.

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Table 1. Variables analyzed to explore their relationship with tiger hunting performance in the study sample.

Variable	Categories	Description
Camp	Camp A	100 ha fenced enclosure. Abundance of bushes in open areas
	Camp B	100 ha fenced enclosure. Absence of bushes in open areas
Gender	Male	
	Female	
Age	Sub-adult	2 to 4 years old
	Young adult	4 to 6 years old
	Old adult	Over 8 years of age
Upbringing history	Zoo-born	Born in Chinese zoos. Never exposed to prey while with mother. Exposure to live prey for the first time while with another tiger of similar age and with no hunting experience
	5 months	Born at LVR. Brief exposure to live prey (i.e., four occasions) while with mother. Separated from her at the age of 5 months of age
	13-15 months	Born at LVR. Repeated exposure to live prey while with mother. Separated from her at 13-15 months of age
	Hand-reared	Born at LVR but rejected /abandoned by mother. Hand-raised and rejoined mother and/or siblings at 9 months of age
Mother	Mother	Cubs spent a certain amount of time with their mother, that varied from tiger to tiger, while being exposed to live prey
	No mother	Cubs never spent any time with their mothers while being exposed to live prey

Table 2. Hunting performance of captive-born South China tigers at Laohu Valley Reserve (South Africa). Data are presented in decreasing order of blesbuck kill rate for each tiger in Camp A. The number of times fed by humans depended on the condition of the tiger under consideration. If a tiger had not killed blesbuck for six days and started to show indicators of poor body condition (see text for further details), the tiger was fed a small portion (i.e., 6-8 kg) to avoid further loss in body condition.

		Camp A					Camp B				
Tiger	Sex	Nights in enclosure	Number of blesbuck kills	Blesbuck kill rate (days/kill)	Other species kills	Number of times fed by humans	Nights in enclosure	Number of blesbuck kills	Blesbuck kill rate (days/kill)	Other species kills	Number of times fed by humans
T1	M	22	7	3.14	0	0	25	0	-	1	3
T2	F	34	7	4.86	3	1	22	1	22.00	0	0
T3	F	20	4	5.00	1	0	29	3	9.67	1	2
T4	M	23	4	5.75	0	0	23	0	-	3	1
T5	F	23	4	5.75	0	0	21	0	-	2	2
T6	M	21	3	7.00	0	0	24	5	4.80	0	0
T7	F	22	3	7.33	0	0	20	1	20.00	0	3
T8	M	21	2	10.50	2	0	21	0	-	2	2
T9	F	21	2	10.50	0	0	23	1	23.00	0	2
T10	M	23	2	11.50	0	0	20	0	-	1	1
T11	M	21	1	21.00	2	0	21	0	-	0	0
T12	M	9	0	-	0	0	22	0	-	2	0

Figure 1. Study area showing the enclosures (Camp A and Camp B) that were used to test tiger hunting performance and the importance of stalking cover in hunting success for this species (Laohu Valley Reserve, Free State Province, South Africa).

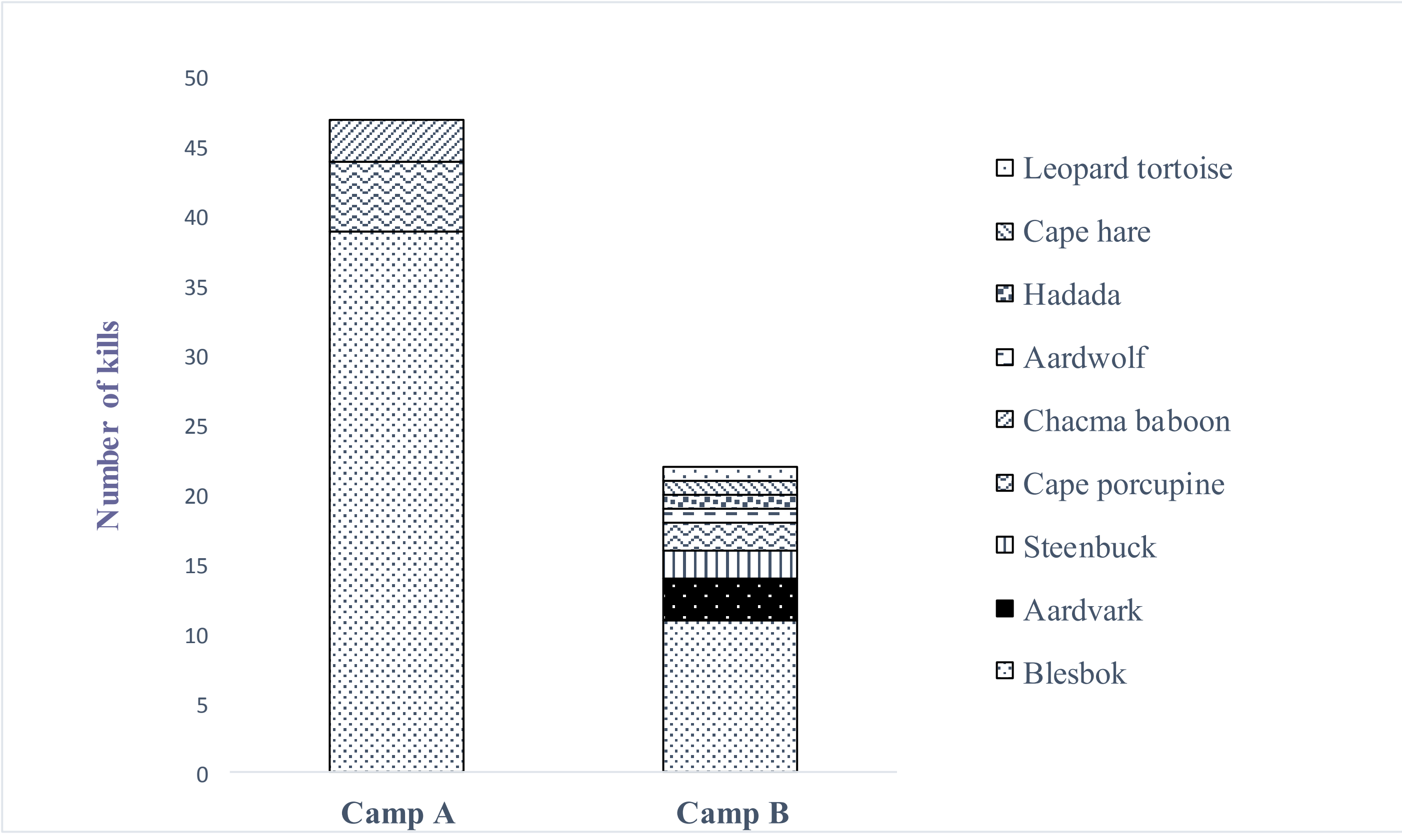

Figure 2. Number of kills and species hunted by tigers over the study period (n= 12 tigers). Species hunted included: leopard tortoise (*Stygmochelys pardalis*), Cape hare (*Lepus capensis*), hadada (*Bostrychia hagedash*), aardwolf (*Proteles cristata*), chacma baboon (*Papio ursinus*), Cape porcupine (*Hystrix africaeaustralis*), steenbuck (*Raphicerus campestris*), aardvark (*Orycteropus afer*), and blesbuck (*Damaliscus pygargus*).

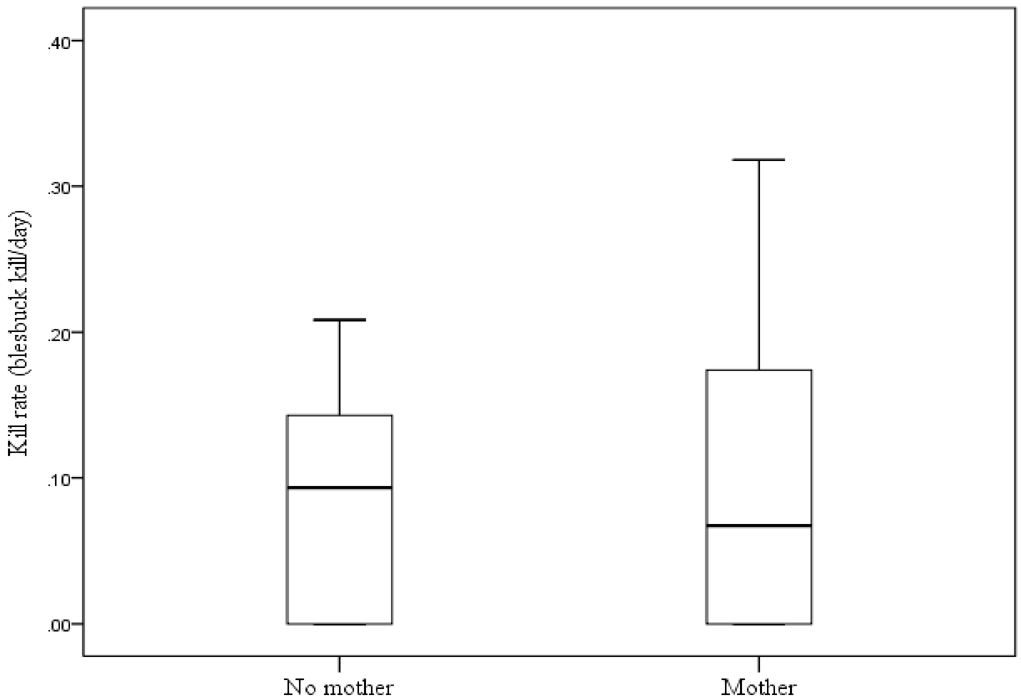

Figure 3. Tiger hunting performance expressed as blesbuck kill rate (blesbuck kills/day) and grouped according to whether the tiger had the presence of its mother while exposed to prey in early development (n=12 tigers).

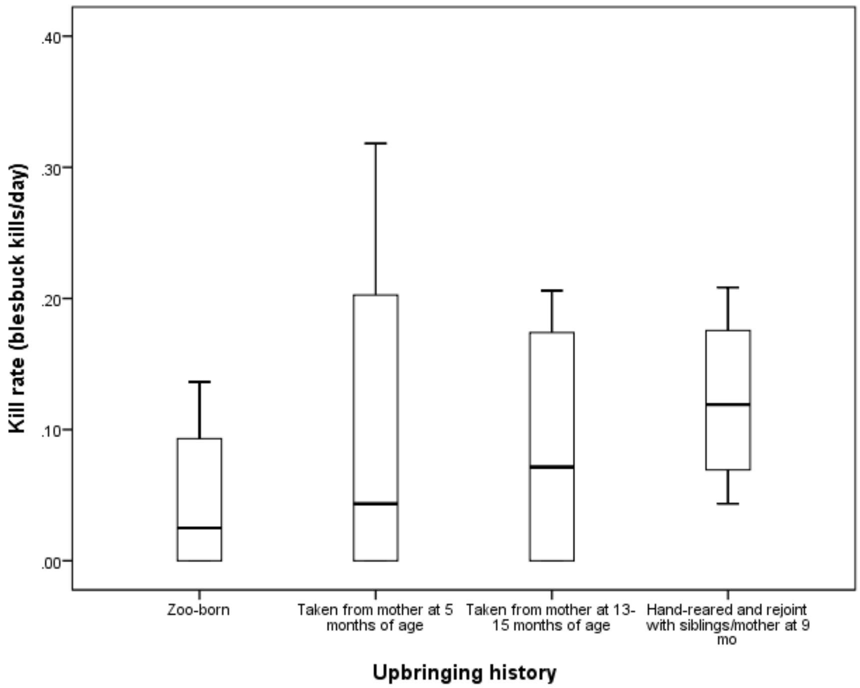

Figure 4. Differences in tiger kill rate (blesbuck kills/day) according to upbringing history (n=12 tigers).