

African lion trophy hunting policy cannot be based on a site-specific model

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Abstract

We assess a simulation model that proposed a sustainable trophy hunting method for African lions based on a long-term study of lion biology in Tanzania. The model predicted no discernible effect of harvesting males ≥ 6 yr from a population, and suggested that numerical hunting quotas be replaced with age-based quotas. According to the model, lion age could be reliably estimated using nose colour, because lion noses in Tanzania darkened "predictably" with age. By limiting offtake to only those males with noses $> 50\%$ black, hunting could theoretically be restricted to animals of an appropriate age. We provide information based on a 10+ yr study in Botswana showing no statistically significant pattern of nose darkening with age for southern African lions. In addition, we show that male reproductive parameters in our study population differ significantly from those in the Tanzanian population. Specifically, in comparison with eastern African lions, male lions in southern Africa (1) disperse from their natal prides at later ages; (2) take over prides at later ages; and (3) have multiple reproductive opportunities after their tenure with an initial pride. Given these regional differences in both nose colour variation and male reproductive behaviour, we caution against a pan-African acceptance of age-based quotas. We strongly advise that any simulation model of sustainable hunting practice integrate regionally specific information.

Introduction

The decline in population numbers of African lions (*Panthera leo*) has been precipitous in both historical and recent times. Chardonnet (2002) and Bauer and van der Merwe (2004) recently estimated a continental population of 16,500 to 47,000 individuals. Such estimates were perhaps necessarily based on little more than educated guesses and various forms of extrapolation for most reporting locations; nevertheless, these approximations represent a highly significant decline in similarly estimated population numbers twenty years ago (Ferrerias and Cousins 1996; Nowell and Jackson 1996). The causes for this decline include loss of habitat, direct persecution by humans protecting livestock resources, and a reduction of prey base, all of which are directly attributable to increasing human populations in Africa and a consequent reduction of wildlife habitat (Woodroffe 2000; Patterson et al., 2004). Currently, management of conflicts between humans and large predators is considered one of the most critical conservation issues for such species (Saberwal 1994; Patterson et al., 2004), although disease issues in protected areas and edge effects will also play a significant role in conservation and management of remaining lion populations (Packer et al., 1999; Kissui and Packer 2004; Troyer et al., 2004).

Governments, non-governmental organizations, and commercial safari operators continue to recognize the direct use value of lions. An analysis conducted in Amboseli National Park expressed the net value to the national economy of a single adult male lion as \$515,000 from safari viewing (Thresher 1981). In Botswana, trophy hunters paid in excess of \$50,000 for a 3-week safari that includes a trophy-quality male lion (ULG 2001). In Tanzania, Creel and Creel (1997) estimated that industry revenue from trophy hunting (government and hunting

companies) in 1992 was \$13.96 million, and that 12-13% of this total was generated by lions. Proponents of trophy hunting point out that such activities contribute to continued existence of lion populations in non-protected areas lacking sufficient infrastructure or game densities to support viable photographic tourism (Lewis and Alpert 1997; Wilkie and Carpenter 1999). In addition, revenue from trophy hunting theoretically provides conservation incentives to communities that incur direct costs (e.g. livestock losses) of living with lions. Such revenue, however, is in many cases absorbed disproportionately by the private sector (i.e. the hunting companies) and government (Kiss 2002). Even when benefits are more equitably distributed, there are doubts whether such revenue leads to increased tolerance of dangerous predators (Murombedzi 1999; Rozemeijer 2003; del Valle 2004). Economic damage resulting from conflict between humans and large predators can lead to reprisals or preventative measures that could threaten population viability of wild species (Madhusudan 2003, Walpole et al., 2003).

Wildlife populations subject to periodic offtake require careful monitoring to ensure that such measures are sustainable. Complex social dynamics of lions make setting of any quota difficult, as incoming males disrupt pride structure in a number of ways, including infanticide of cubs not related to them (Bertram 1975; Packer 2000). Females in a pride need a period of stability in male tenure to be able to raise cubs successfully; trophy hunting is expected to increase the rate of male turnover and thereby decrease both pride stability and overall reproductive output by females (Bygott et al., 1979; Whitman et al., 2004). Studies in Tanzania (e.g. Creel and Creel 1997) caution proposed offtake levels of 10-16% of the adult male population.

Within this context, a recent publication by Whitman et al. (2004) proposed a computer simulation model for sustainable lion trophy hunting based on an age quota rather than a numerical quota. The authors suggested that male lions reach sexual maturity at 2.5 yr, and are capable of taking over prides at 4 yr. They allowed that male lion coalitions need to remain within pride territories for two years to allow their offspring to attain a level of reduced vulnerability to mortality from incoming males (Pusey & Packer 1994). This model subsequently concluded that trophy hunting is likely to have minimal impacts on lion populations if offtake is restricted to males that are no younger than 6 yrs. The model acknowledged the possibility of infanticide, but the authors concluded that ‘as long as hunting is restricted to a safe minimum age ... there is no risk of setting excessive quotas even in areas where it is impossible to estimate the overall population size’ (Whitman et al., 2004).

Age determination among free-ranging lions is complex, and is perhaps most reliably approximated by dental characteristics such as determination of incremental cementum line counts for canine root sections (Smuts et al., 1978). A diversity of other measures has also been used, including tooth wear and loss, tooth discolouration, skull and mandible measurements, etc. (Smuts et al., 1978). The reliability of such techniques has not been assessed across environments and populations, and these methods have limited applicability in determining the age of lions while they are alive.

Whitman et al. (2004) therefore proposed a means of aging live lions based on nose colour. By analyzing digital photographs of known-age lions in the Serengeti and Ngorongoro Crater, Tanzania, Whitman et al. (2004) showed a correlation between lion age and the proportion of the

lion's nose tip which is black in colour. The authors suggested the simple 'rule of thumb' that a lion whose nose is 50% black is estimated to be ≥ 5 years old. Removal of males of this age or older from the population, according to their simulation models, would not affect population stability and thus would constitute a sustainable trophy hunting practice.

While Whitman et al. (2004) acknowledge that both (1) the schedule of lion nose-darkening and (2) the reproductive parameters defining the simulation model may be site-specific, their recommendations have had considerable impact on trophy hunting and management policies (e.g. Packer et al., 2006). Data generated in Tanzania must therefore be evaluated for robustness using site-specific data from lion populations in different geographic locations and/or habitats. Funston et al. (2003) have already provided information to indicate that male lions in South Africa (Kruger National Park) take over prides at a later age than in the Serengeti and have a considerably longer reproductive life than integrated into the simulation model of Whitman et al. (2004).

We present here information demonstrating the extent of such site-specificity, highlighting differences between the suggestions of the Whitman et al. (2004) model and data gathered from our study population in northern Botswana. We show that nose colour is not a reliable indicator of lion age in northern Botswana, using two different methods of analysis (one based on visual inspection and one based on computer analysis of digital photographs). Additionally, we present data demonstrating that male reproductive parameters differ substantially between Tanzanian populations and our study population in Botswana, and that such differences challenge the general applicability of the Whitman et al. (2004) model to lion populations outside Tanzania.

Methods and Materials

All data is based on our long term (10 yr) study of lions in the Okavango Delta region of northern Botswana, one of the few areas in Africa still supporting a significant lion population (Bauer and van der Merwe 2004). Our evaluation and analysis includes both the reliability of nose pigmentation as an indicator of lion age and male lion reproductive assessments.

Nose colour assessment: visual analysis

Individual identification of lions has been based on a number of techniques, including scars, ear notches, and spot patterns above the top whisker row (Schaller 1972; Rudnai 1973). As such distinctions are likely to change over time (healing of scars, addition of notches, facial scarring obscuring whisker patterns especially among males), we added two other identification determinants to our standard methodology: (1) individually variable dark pigmentation of the gums in front of and behind the lower incisors, and (2) nose pigmentation. This diversity of information on individual identity allowed us to confidently identify nomadic lions, for example, that would only occasionally be encountered in the study area over a period of several years.

Historically, nose colour for each lion in our study area has been classified as ‘pink’, ‘black’, ‘pink/grey’, or ‘pink with dark spots’ (see Figure 2 for examples of lion noses from each of these colour categories.) Nose colour was assessed for a total of 149 known-age lions (81 females and 68 males). For this analysis, lions were classified into five age classes (0-1 yr, 1-3 yr, 3-5 yr, 5-7

yr, and 7-10 yr). Nose colour was only recorded when each individual was first identified, and therefore the results represent a series of single observations rather than a longitudinal assessment of nose colour. (This is in accordance with data presented by Whitman et al. (2004) for Tanzanian lions.)

This method of lion nose colour assessment is admittedly susceptible to human error or subjective differences of opinion. However, Whitman et al. (2004) suggest that lion age can be reliably estimated by hunters visually evaluating and quantifying the darkness of a lion nose. We therefore feel that our method of visual assessment is valid within this context as a mechanism for detecting age-related patterns of nose colour variation.

Nose colour assessment: pixel analysis of digital photographs

As in Whitman et al. (2004), nose photographs were taken of both male and female known-age lions. In all, 52 digital photographs were analyzed (30 female and 22 male), representing a total of 42 lions (24 female and 18 male). Age was determined in most cases from known birth date, but occasionally for females by extrapolating backward from age at first reproduction. When considering lions for which we had multiple photographs, we followed the methods of Whitman et al. (2004), and included for analysis only an average of values for both lion age and nose darkness.

The fleshy ‘nose tip’ area of each photograph was excised using Microsoft Paint (see Figure 1). A pixel analysis of the nose tip was performed using a MatLab program designed specifically for this purpose. Each nose tip was broken down into its constituent pixels, and pixels were

individually represented in terms of their computer-assigned RGB values. (RGB is a standard computer-based assessment of colour comprising three numbers that represent the amount of red, green and blue in an individual pixel. A RGB value of [0,0,0] is pure black, and an RGB value of [255,255,255] is pure white.)

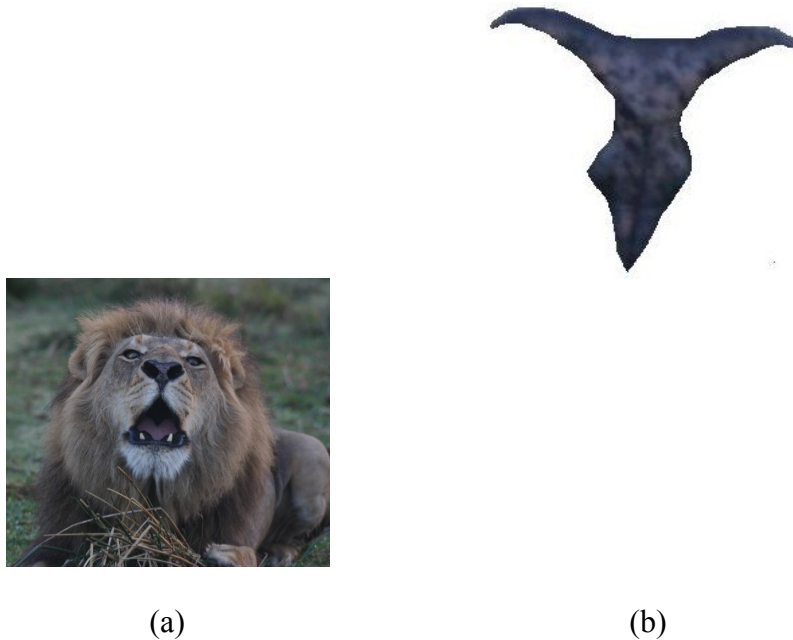


Figure 1. (a) Digital photograph of male lion, age 7.5. (b) Excised nose tip used for pixel analysis.

Pixels were then analyzed using a number of different definitions of the threshold for considering any particular pixel to be ‘black’. There are very few cases in which a pixel in a digital photograph will have the RGB value of [0,0,0] because the colour ‘pure black’ rarely occurs in nature. As a result, we tested various different definitions of ‘black,’ involving different threshold values of a darkness parameter (DP) defined as $DP = (R+B+G)/3*255$. The lower the DP threshold, the more ‘restrictive’ the definition of which individual pixels qualified as ‘black’.

The relevant result, ‘proportion black,’ was then defined as the proportion of pixels in a given nose tip photograph which had DP values less than or equal to the chosen DP threshold. For instance, at a DP threshold of 0.25, a ‘proportion black’ of 0.17 means that 17% of the pixels in that photograph have DP values at or below 0.25 and are therefore defined as ‘black.’ See Figure 2 for example lion noses with corresponding values of ‘proportion black’.

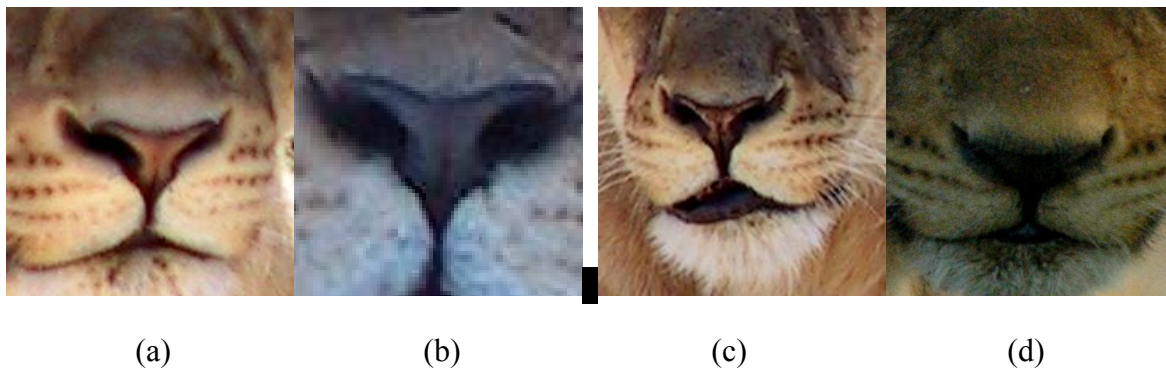


Figure 2. Examples of both visual and computer colour analyses of lion noses. (a) 2.25-year-old female; proportion black = 0.0582, visual colour category = pink. (b) 10-month-old female: proportion black = 0.1229, colour category = pink/grey. (c) 7.2-year-old female: proportion black = 0.2281, colour category = pink spotted. (d) 8-month-old male: proportion black = 0.9913; colour category = black. Note that values of ‘proportion black’ are given for a DP threshold of 0.25.

We also attempted to calibrate darkness values to correct for the overall darkness or lightness of the photograph. A photograph taken of a lion in direct sunlight might skew results when compared to photographs taken of the same animal in shade. We therefore divided ‘proportion black’ by the average darkness (average DP value) of the entire photograph, and compared a plot of this new ratio to the original plot of uncalibrated ‘proportion black’. This calibration did not noticeably alter the relationship between ‘proportion black’ and age. We therefore concluded that the overall lighting of the photograph did not significantly affect our results.

Male lion reproductive parameters

Data on ages of males at pride takeovers, reproductive success based on length of tenure, and fate of previously resident males after losing prides is based on over 2700 locations of lions during the 10-year study, conservatively representing over 5000 hours of observation. Data from such observations has been presented previously (Kat 2001), but are here augmented to represent an additional four years of study.

For this analysis, we considered a takeover (replacement of resident males) to have occurred when new males were observed to be in the regular presence of pride females, even though previously resident males might still be present within the pride territory. With few exceptions, such takeovers did not include overtly aggressive interactions between newcomers and previous pride males except for occasional chases and frequent vocalizations. Incoming males had frequently been encountered by us within pride territories several months before the eventual takeover, and pride takeovers in many instances involved movements of known males from neighbouring territories.

In addition, we noted several consecutive takeovers by resident pride males that either tried to add neighbouring prides to their original territories or abandoned original prides in favour of neighbouring prides. In each case, such successive takeovers were considered as separate events, even though they involved known male coalitions.

According to our own data and that presented in Pusey and Packer (1994), we considered that cubs aged >2 yr had a significantly greater chance of surviving pride takeovers than younger

cubs. Reproductive assessment compared to length of male tenure is therefore based on the number of cubs that survived to >2 yr.

Results

Nose colour assessment: visual analysis

Nose colour assessments of 149 lions of different sexes and ages are presented in Figure 3.

Several inferences can be made from this data. First, cubs are born with a diversity of nose colours, ranging from pink to black. While pink and pink/grey noses dominate percentage-wise in the sample of cubs, such results contrast with the assumptions of Whitman et al (2004) suggesting that all lions are born with noses of an overall light colour which then darken with age.

This diversity of nose colours continues to be represented in lions of all ages. Nevertheless, there is an increase in the proportion of black noses among older lions as well as an increase in the percentage of pink spotted noses in older lions. It should be noted, however, that the diversity of nose colours even in the oldest age category (7-10yrs) suggests that there is no reliable ‘schedule’ for an overall increase in pigmentation with age as proposed by Whitman et al. (2004).

The absence of black noses among lions 3-5 yrs old is probably no more than a residue of our decision only to note nose colour when lions were first categorized. This therefore does *not* mean

that cubs born with grey or black noses lose their pigmentation as they age, only to gain such pigmentation again later in life.

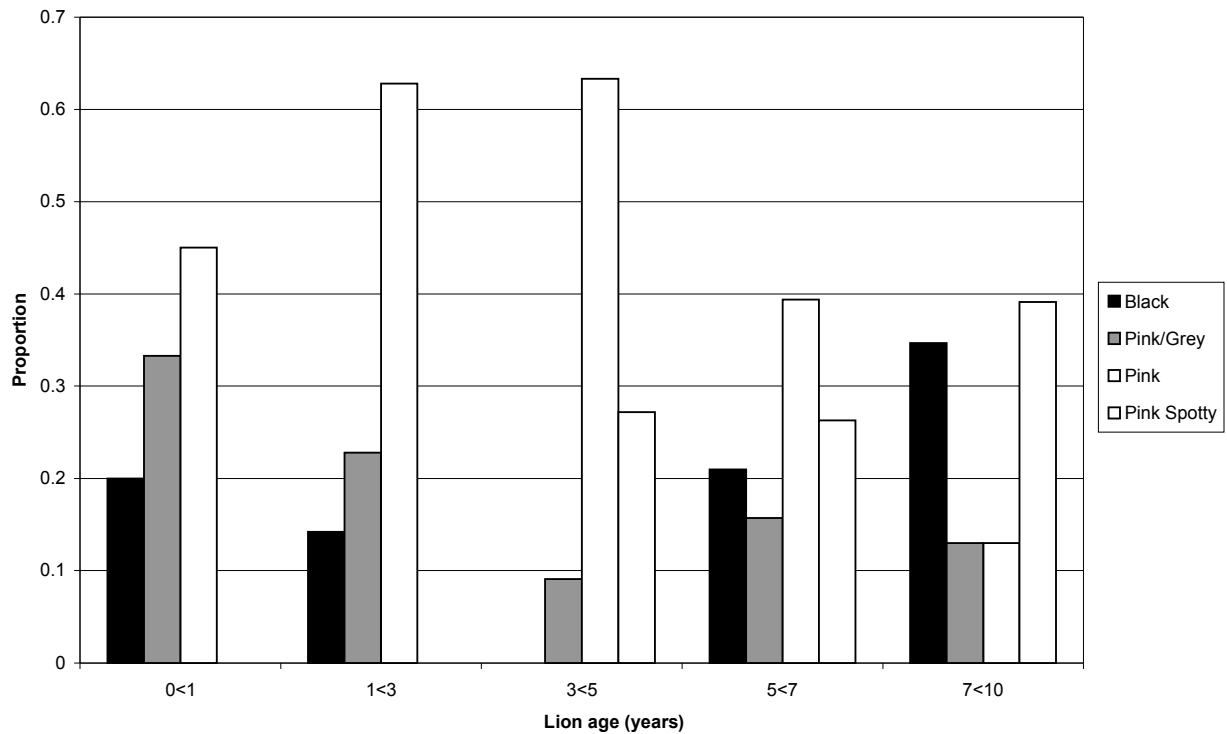


Figure 3. Diversity of nose colour classes among all lions (n=149). Age classes include lions 0-1 yr (n=29), 1-3 yr (n=42), 3-5 yr (n=20), 5-7 yr (n=37), 7-10yr (n=21).

Nose colour assessment: pixel analysis of digital photographs

We were unable to find any reliable correlation between nose darkness and age in our lion population. For all permutations (all lions, females only, and males only), as well as each DP considered, there appeared to be a slight general positive relationship between age and overall dark nose colour. However, R^2 values revealed that these correlations were in no way statistically

meaningful. The highest R^2 value using any measure of analysis was 0.3073 (females only, $DP=0.25$), indicating a very weak relationship between nose darkness and age. Figure 4 presents a scatterplot of nose darkness versus age using a DP threshold of 0.25, representing an intermediate restrictiveness of the definition of 'black.'

A lack of reliable correlation between nose colour and age was also clear when the analysis considered only male nose colour ($R^2 = 0.1748$). Since the stated purpose of aging lions using nose colour is to identify potential trophy males, the correlation between nose colour and age must be especially strong in male lions in order for this criterion to be useful. It is worth noting that while Whitman et al's (2004) trend towards overall nose darkening with age was based on a large number of lions, only eleven male lions over the age of five (3 from the Serengeti and 8 from the Ngorongoro Crater) contributed towards the overall conclusions. The correlation of nose darkness with age was predominately established by female lions.

Of the 18 males considered in our study, 8 were over the age of 5. Proportion of nose blackness for these 8 males ranged the entire spectrum from 0 to 0.98. Of the total 18 males considered, 5 had noses which were over 50% black (according to DP threshold = 0.25, a definition of 'blackness' which was mid-range in terms of restrictiveness). Males with such nose colours ranged in age from 8 months to 9.5 years.

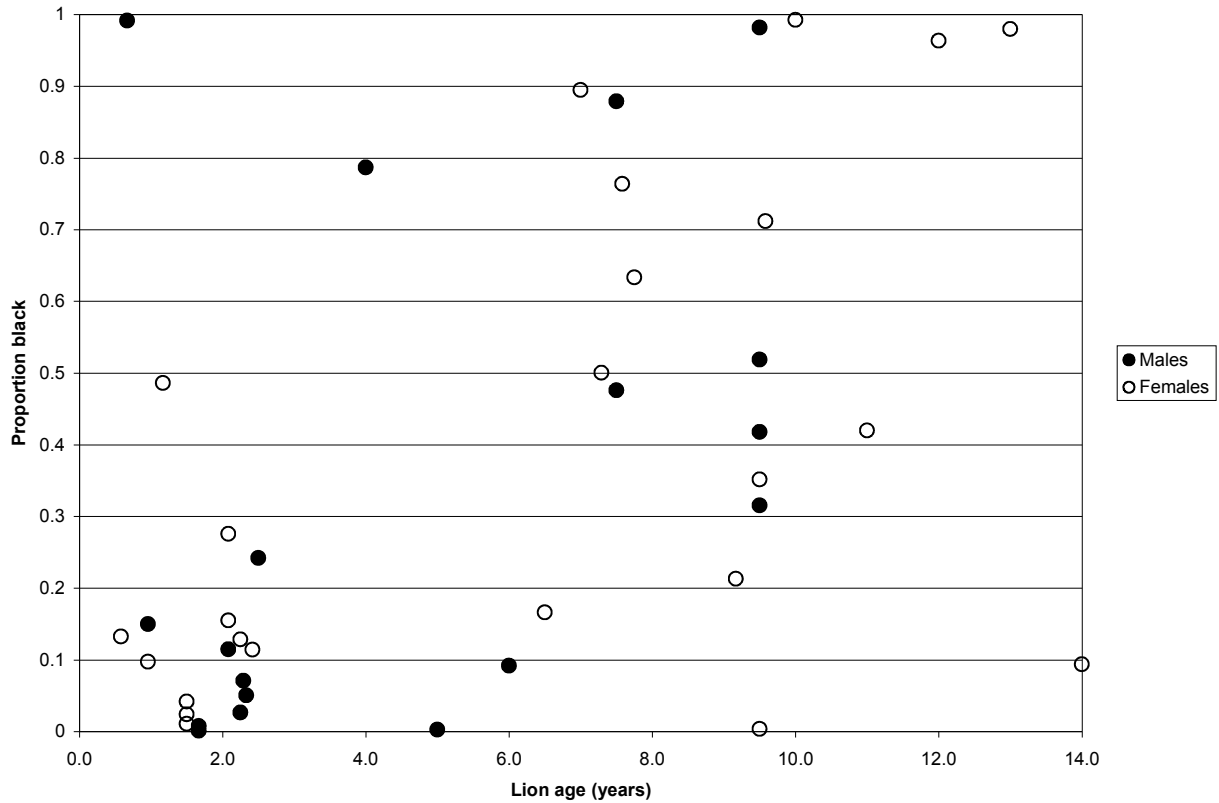


Figure 4. Nose colour variation for all lions (n=42), DP threshold = 0.25. This threshold represents an intermediate level of restrictiveness in defining pixels as ‘black’. Note the general positive correlation between proportion black and age, but the low statistical correlation ($R^2 = 0.25$ for all lions; 0.17 for males only; 0.31 for females only). Also note that of the 8 males over the age of 5, ‘proportion black’ ranges from 0 to 0.98. Of the 5 males with noses over 50% black, ages range from 8 months to 9.5 years.

Male lion reproductive parameters

From 1996 to 2006, 19 male coalitions have been established in the study area. Average coalition size is 2.4 (range 2 – 4 males). Males have an average tenure of 21.7 mo (range 6 – 35 mo, n=15 coalitions). Average male age at time of pride takeover is 7.8 yr (range 5.5 – 11.8 yr, n=18 coalitions).

Average age of dispersal of young males from natal prides is 45.5 mo in our study area (range 30-59 mo, n= 8 groups of dispersing males). Age of dispersal is complicated by several factors. First, young males tend to make several sorties away from their natal pride territory, often associating with unrelated males of similar age before returning to their original pride areas for variable periods of time. We did not recognize such initial sorties as true dispersal events. Final dispersal age was calculated from date of birth to date of last being seen in natal pride territories. Second, age of dispersal of young males was to some extent influenced by the number of like-aged males in a cohort and the timing of their mothers giving birth to a new litter of cubs by incoming pride males. Such adult males tended to be aggressive to subadult males in their newly acquired territories, although this was not ubiquitously the case. A singleton male born into one of our study prides continued to associate with pride females even in the presence of incoming males, and took the longest time to eventually disperse (59 mo). In contrast, a group of three males took the shortest time to disperse (30 mo) after their mothers gave birth to new litters of cubs. Age at final dispersal is thus likely to be influenced by a number of factors: (1) reluctance of young males to leave familiar pride territory; (2) aggressiveness by incoming males unrelated to them; and (3) intolerance by females in their natal prides. Nevertheless, this average age of dispersal is higher than that noted in the Serengeti (36 mo average, with a maximum age of 65 mo (Hanby and Bygott 1987)), but is comparable to similar data from Kruger National Park in South Africa (40 mo average, maximum age 60 mo (Funston et al., 2003)).

After taking over a pride, there is a characteristic lag period before females give birth to cubs sired by the incoming males. Packer and Pusey (1983) mentioned that in their study in the Serengeti this lag period amounted to a median of 244 days (n=5 takeovers), and in this study the

delay amounted to an average of 231 days (n=9 takeovers with successful reproduction; range 120-300 days until the first female in the pride gave birth). The gestation period of female lions has generally been accepted to be 110 days on average (Schaller 1972; Packer and Pusey 1983). In our study, it was noted that male lions take an average of 14 mo to begin exploring neighbouring territories, perhaps opportunistically mating with resident females, but then always return to their original territories (Kat 2001). As stated above, we did not consider such exploratory moves as takeovers until we had clear evidence that males originally resident in such exploratory territories had been ousted.

While male lions are not involved in raising cubs, it is generally accepted that the duration of male tenure is critical to the reproductive success of female lions because pride males prevent possible incursions by other males. Packer and Pusey (1983) estimate that 'a female needs to be protected from [unrelated] male harassment of her cubs for at least 25 mo if she is ever to raise offspring'. Bertram (1975) indicated that cubs reaching 2 yr generally survived to adulthood. If data gathered in this study are analyzed by tenure length and number of cubs surviving >2 yr, results are in general agreement with Packer and Pusey (1983). Increased tenure length is correlated with a higher number of surviving cubs produced, and no cubs survived in coalitions where tenure length was less than 20 mo (see Figure 5). Such data are doubtless influenced by the number of reproductive females in any particular pride where males establish tenure, although the correlation is not improved when proportion (as opposed to number) of cubs surviving >2yr is plotted against male tenure length (not shown).

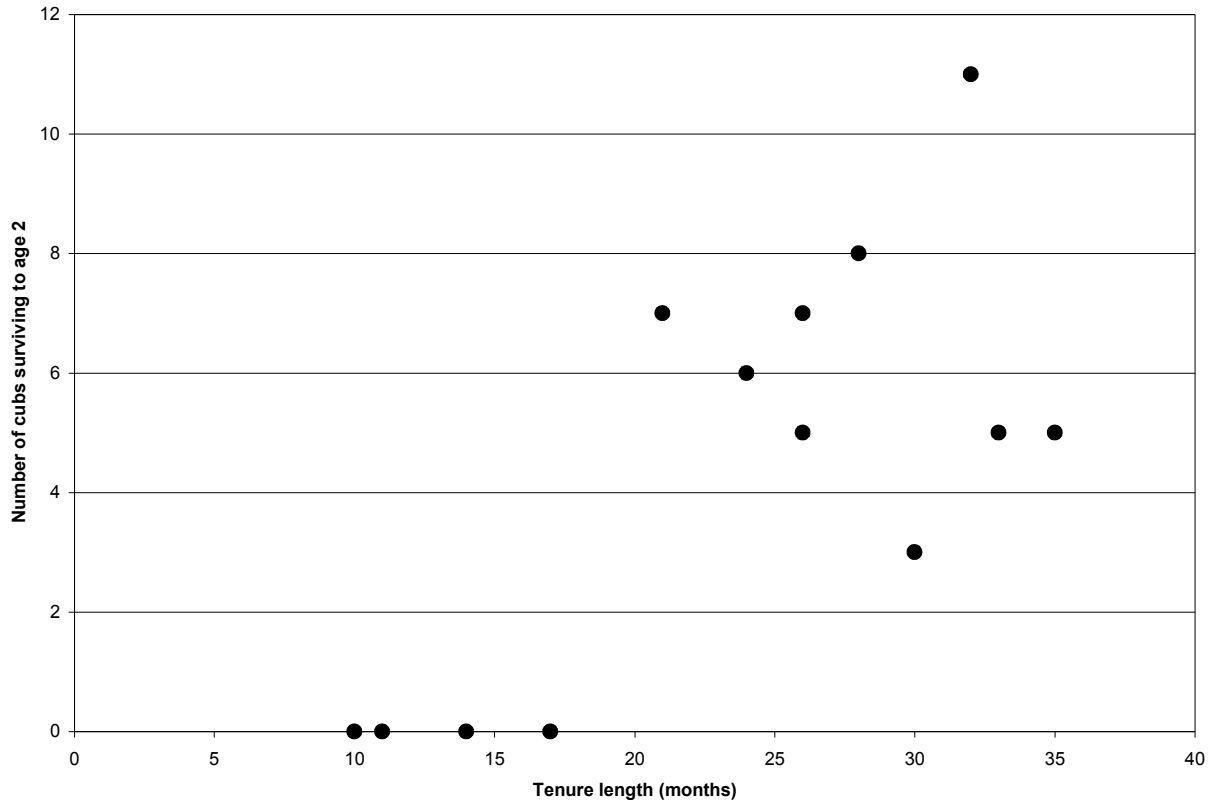


Figure 5. Effect of male tenure length on cub survival. Note the overall trend towards greater number of cubs surviving with increased tenure length ($R^2 = 0.53$). Also note that no cubs survived a tenure length of less than 20 months.

In addition to length of tenure, age of males at takeover also seems to play an important part in the number of cubs raised to >2 yr. Older males taking over prides show a trend towards shorter tenures than younger males and therefore sire fewer cubs (correlation = -0.70). Such data is influenced by the fact that older males tended to take over smaller female groups resident in the study area.

Seven successfully established male coalitions attempted to run two prides simultaneously after having taken over their first pride. Three of these coalitions returned to their original prides when new males appeared in the area of the second pride; one coalition was ousted after the death of a

coalition member; two coalitions abandoned their first pride in favor of the females in their second pride; and one coalition is still resident in the area, associating and mating with four groups of females.

In all cases where one male in a coalition of two died during tenure, the single surviving male was always subsequently ousted by incoming coalitions. Of five coalitions of two males where a coalition partner was killed (2 unknown causes, 1 due to disease, 1 due to trophy hunting, 1 due to other male lions), four formed new coalitions, always with younger males unrelated to them. Among these five coalitions ousted when coalition partners died, remaining members were encountered in the study area for an average of 24.2 mo (range 16-33 mo) after the partner's death. Four such singleton males subsequently associated and mated with either females from the prides they had been ousted from or females from neighbouring prides. One coalition, originally numbering four males (ultimately reduced to two males after one male died of disease 5 mo after the initial takeover, and after a second male was killed by other male lions 26 mo after initial takeover), remained in the study area for at least 73 mo, taking over and reproducing with females in three prides.

Discussion

Nose colour and age

Based on two different methods of analysis (one visual, one computerized), we conclude that there exists no reliable correlation between nose colour and age in our study population of lions in northern Botswana. Visual assessment of nose colour indicates a considerable diversity among lions of all ages, although we do note a trend towards an increase in the proportion of

black and pink spotted noses among lions in the oldest age class (7-10 yr). Neither this study nor that of Whitman et al. (2004) evaluated single individuals over time to allow evaluation of the hypothesis that lion noses darken with age. We suggest, however, that given the diversity of nose colours noted among lions of all ages, a specific and age-dependent schedule of nose darkening is not applicable to lions pan-Africa.

Computer-assisted evaluation of the degree of ‘blackness’ among lion noses suggests similar results. Regardless of the various levels of permissiveness of our definition of ‘black’, we are unable to find a statistically meaningful relationship between nose colour and age, despite a general trend towards darkness with age as noted in the visual evaluations. As with the visual evaluations, individual variation in nose colour is far too great to allow any type of reliable age assessment based on nose colouration. Although Whitman et al. (2004) found an overall strong correlation between age and ‘blackness’ of noses in the populations examined in East Africa, we would not recommend this measure to be ubiquitously applied to all lion populations in Africa. We judge this criterion too unreliable and site-specific to be useful as a general measure of lion age, either for research or trophy-hunting purposes.

Male reproductive parameters

We suggest that the model for sustainable trophy hunting of male lions proposed by Whitman et al. (2004) must be re-evaluated by considering data on male reproduction and dispersal from southern African populations.

Whitman et al (2004) propose that male lions are capable of reproducing at 30 mo. We suggest that lions of this age might have reached puberty, but have not achieved the necessary body size to challenge resident adult males to take over a pride. Indeed, data from the Serengeti indicates that average age of male dispersal from their natal prides does not occur before 32-36 mo, with some young males staying with their pride in excess of 48 mo (Schaller 1972; Pusey and Packer 1987). Hanby and Bygott (1987), also analysing data from the Serengeti, arrived at an average dispersal age of 36 mo, with a maximum of 65 mo. Data from southern Africa (Funston et al., 2003) indicates that dispersal of young males takes place at an average age of 40 mo, with a maximum of 60 mo. Our study of Botswana lions shows that young males disperse at an average age of 45.5 mo, with a maximum of 59 mo, which is in general agreement with the data provided by Funston et al. (2003). Thus young male lions, while perhaps attaining puberty at 30 mo, are most likely still with their natal prides at this age, whether in eastern or southern Africa. Importantly, however, male dispersal appears to occur at a later age in southern African lion populations than eastern African populations (45.5 mo versus 36 mo).

Whitman et al. (2004) also propose that male lions take over prides at 4 yr, and then can be harvested from the population at 6yr. This assumption acknowledges that female lions in a pride require at least 2 yr to raise cubs to a relative stage of maturity that increases the likelihood of their survival to adulthood. We would caution that while young males in Tanzania might possibly be able to take over prides at 4 yr, this is not the case among southern African lions. Funston et al. (2003) indicate that male takeovers occurred in South African populations at a much later age, and our data from Botswana show that the average age of males when taking

over a pride of females is 7.8 yr (although this data is perhaps skewed by resident males successively taking over different prides in the study area).

The model developed by Whitman et al. (2004) also assumed that male lion coalitions have a single lifetime reproductive opportunity when taking over their initial pride. Bertram (1975) also concluded that in the Serengeti, 'adult males ousted from a pride rarely get possession of a new pride again, and they probably die within a very few years'. Data provided by Funston et al. (2003) and our data suggest that male coalitions continue to have reproductive opportunities even when they are ousted from their initial pride or choose to abandon this initial pride in favour of female groups in neighbouring territories. Indeed, older males in our study area whose original coalition partners have died or been killed will often form new coalitions with younger males and take over subsequent prides. In addition, ousted males will generally remain in their original pride territories and take advantage of mating opportunities with resident females, and/or move into neighbouring pride territories to associate with females there. Such data is reflected by genetic studies performed in the Selous, where relationships among cubs suggest that females often mate with males outside the pride (Spong et al., 2002).

The average coalition size of males in this study (2.4) is smaller than that recorded in the Serengeti (Schaller 1972; Pusey & Packer 1994). A consequence of such small coalitions could be either that ousted intact coalitions have opportunities to take over subsequent prides, or that single ousted adult males can form coalitions with new and younger males to regain reproductive opportunities. We therefore dispute the assumption by Whitman et al. (2004) that male lions have a limited reproductive life and can be sustainably harvested two years after they have taken over

their first pride. We acknowledge that older males sire and raise fewer cubs in prides gained subsequent to their first takeover; however, such males continue to play an important role in overall reproductive success of females in our study area.

The professional hunting community in Botswana has apparently already accepted the model of only taking male lions >6 yr based on nose colour categories (Packer et al., 2006). We have discussed how differences in both nose colour variation and male reproductive behaviour limit the applicability of Whitman et al.'s (2004) trophy hunting model to southern African lion populations. However, there are additional practical reasons to caution against a pan-African acceptance of this model.

First, the success of the model is dependent on hunters using nose colour as a means to reliably age lions. However, even if nose colour were a valid indicator of lion age, a nose colour standard is quite impractical for use in the field assessment of a potential trophy animal. Evaluation of nose colour becomes near impossible under conditions which hunters face when approaching a lion on foot. Interviews with hunters in Botswana (Lincoln, pers. comm.) indicate that the generally shy lions in hunting areas cannot be approached to sufficient proximity to determine if a nose is more than 50% black.

Second, the Whitman et al. (2004) model will eventually result in a manipulated population of hunted lions, in which younger males must assume the reproductive roles of their harvested elders. Such unnatural population demographics might be manageable in isolated areas. However, Botswana and other African nations have elected to border hunting areas directly onto

protected areas; with regular movements of lions between protected areas and hunted areas, such theoretical possibilities for management and manipulation will be impossible.

We therefore conclude the following:

1. While lion nose colour darkness might be a reasonably reliable indicator of age in the Serengeti, there is no statistically reliable relationship between this measure and lion age as assessed by two methods in our study population in northern Botswana. We therefore do not recommend the use of nose colour as a means to assess lion age in southern Africa.
2. Male reproductive parameters in our Botswana study population do not support the assumptions of the Whitman et al. (2004) model for sustainable trophy hunting. In comparison with East African lions, males in southern African lion populations (1) take longer to disperse; (2) take over prides at a later age; and (3) have multiple reproductive opportunities after their tenure with an initial pride.
3. Beyond regional differences in nose colour variation and male reproductive parameters, wide application of the Whitman et al. (2004) model also presents practical difficulties. Regardless of the theoretical applicability of percentage 'blackness' of lion noses, this measure is of doubtful practicality in the field. Additionally, the model requires a level of lion population management that is currently impossible in many African nations, including Botswana.
4. Given these data, we propose that the model suggested by Whitman et al. (2004) be viewed with extreme caution by wildlife managers in areas of Africa outside Tanzania. We therefore urge that despite the conclusions presented by Whitman et al. (2004), the

overall management of sustainable trophy hunting of lions is best based on local information gathered from long-term research programs coupled with rigorous evaluation of impact of such offtake on resident populations. Researchers, hunters, and governments should collectively evaluate such information without bias, and evaluate management strategies accordingly.

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