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The relative importance of trophy harvest and retaliatory killing of large carnivores: South African leopards as a case study

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There are considerable challenges in the conservation of large carnivores, caused by large area requirements, low reproduction rates and low population densities coupled with their tendency to cause conflict with humans. Trophy hunting is one strategy to increase support for large carnivore conservation. Leopards, *Panthera pardus*, rank among the most sought-after trophies in South Africa. However, trophy hunting has been suggested as partly responsible for leopard population declines, and leopards are also killed in retaliatory actions. In this study we used a stochastic population model to evaluate the relative influences of retaliatory killing and trophy harvest on leopard population persistence, and to assess the sustainability of the current leopard trophy harvest in South Africa. There was a stronger effect of variation in retaliatory killing than of harvest on population persistence. Although we found low extinction risks for South African leopards within 25 years, high risks of population declines across a wide range of simulation scenarios call for concern regarding the viability of the South African leopard population. We suggest that conflict mitigation may be more effective in promoting leopard persistence than restricting trophy harvest, and that accurate estimates of retaliatory killing are necessary for assessments of harvest sustainability.

Key words: trophy hunting, carnivore, adaptive management, simulation models, population viability analysis.

INTRODUCTION

Conservation biologists and wildlife managers face considerable challenges in the management and conservation of large carnivores (Noss *et al.* 1996). Large carnivores have extensive area requirements, low reproduction rates and normally occur at low densities (Purvis *et al.* 2000). Furthermore, protected areas are rarely large enough to maintain viable large carnivore populations (Linnell *et al.* 2001). Therefore, non-protected areas are important in the conservation of large carnivores (Funston *et al.* 2013). However, carnivore populations in non-protected areas are frequently in conflict with rural communities, commercial farmers and game keepers, and retaliatory killing in response to human–large carnivore conflict is common (Woodroffe & Ginsberg 1998; Dar *et al.* 2009; Dickman 2010). Such conflict-related killing can have both direct and indirect demographic consequences for carnivore populations (Treves & Karanth 2003). For example, legal and illegal retaliatory killing of large carnivores can result in the removal of mature, reproductively active individuals (Woodroffe & Frank 2005; Baker *et al.* 2008). Retaliatory killing can thus hamper carnivore population sustainability as well as impede the recovery of threatened populations (Woodroffe & Frank 2005; Kaczensky *et al.* 2011).

Commercial exploitation, like trophy hunting, is often used as an incentive in non-protected areas to increase local tolerance towards large carnivore populations (Lewis & Jackson 2005; Treves 2009). Appropriately managed trophy hunting can contribute significantly to local economies, and financial returns from hunting may in some cases exceed the cost of predation (Lindsey *et al.* 2012; Funston

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et al. 2013). Trophy hunting may therefore be a powerful financial tool to increase persistence and population viability of some large carnivores in non-protected areas (Funston *et al.* 2013). However, the effectiveness of trophy hunting as a viable conservation tool relies on harvest at demographically sustainable levels (Packer *et al.* 2009). While trophy hunting may not generally pose a major threat to wildlife populations (Lindsey *et al.* 2007), it has been suggested that poorly managed trophy hunting quotas can be a contributing factor for causing declines in populations of some large carnivores (*e.g.* Packer *et al.* 2009; Packer *et al.* 2011). Furthermore, the sustainability of trophy hunting can be adversely affected by retaliatory killing (Loveridge *et al.* 2009). It is therefore important to evaluate the importance of retaliatory killing and trophy hunting simultaneuously when evaluating the sustainablity of harvest levels.

Leopards (*Panthera pardus*) are widely distributed throughout South Africa (Friedmann & Daly 2004) and they are frequently killed in conflict with livestock or game farmers (Inskip & Zimmerman 2009; Thorn *et al.* 2012). Trophy hunting is often seen as an appropiate incentive to conserve leopards (Lindsey *et al.* 2007; Funtson *et al.* 2013), but concern over the sustainability of leopard trophy hunting in South Africa has been raised (Balme *et al.* 2009). These concerns are founded in a doubling of the harvest quota since 2005 (75 to 150 animals), as well as increased incidents of legal and illegal retaliatory killing (Daly *et al.* 2005). Coupled with recent concerns that poorly managed trophy hunting may be partly responsible for declining leopard populations (Balme *et al.* 2009; Packer *et al.* 2011), there thus appears to be a need for a formal evaluation of the sustainability of the current trophy harvest of South African leopards.

Population viability analyses (PVA) are commonly used to evaluate the effects and importance of management actions, like trophy hunting, on population persistence (Reed *et al.* 2002). The interpretability of a PVA is, however, dependent on the quality of underlying population parameters (Dalerum *et al.* 2008). Since such demographic data typically are limited for large carnivores, including leopards (Daly *et al.* 2005), it is often difficult to interpret results from PVAs for these species. A potentially effective PVA method for such situations is to combine stochastic population models with logistic regression (McCarthy *et al.* 1995; McCarthy *et al.* 1996). This approach provides a qualitative assessment of the influence of demographic parameters on extinction risk, and can be used to estimate risk over a wide range of potential demographic and intervention scenarios. It also has the additional advantage that it allows for assessments of interactions among parameters (Cross & Beissinger 2001; Dalerum *et al.* 2008).

In this study we combined binary output from a stochastic population model with logistic regression to evaluate the effects of different scenarios of harvest and retaliatory killing on leopard population persistence, with the dual aim of (i) qualitatively assessing the relative importance of trophy hunting and retaliatory killing for a large carnivore species, and (ii) assessing if the current CITES quota is a cause of concern for the South African leopard population under realistic ranges of population sizes and retaliatory killing.

MATERIALS AND METHODS

Model structure

Rather than trying to provide numerical values for recommended harvest levels, we used a qualitative simulation approach where we focused on evaluating the effects of different combinations of retaliatory killing and harvest scenarios on population persistence (Starfield 1997; Pe'Er *et al.* 2013). This approach allowed us to evaluate uncertainty in retaliatory killing over a range of potential levels of trophy harvest.

We used a previously described stochastic population model with a simple sex and age structure (Dalerum *et al.* 2008). The model can be defined as:

$$P_t = AM_t + AF_t + SM_t + SF_t + J_t \quad (1)$$

where P_t is population size, AM_t and AF_t is the number of adult males and females, SM_t and SF_t is the number of subadult males and females, and J_t is the number of juveniles at year t, respectively. The model is temporally discrete with time steps of one year. Following Swanepoel *et al.* (in press), we regarded animals older than three years to be adults, animals between one and three years to be subadults and animals less than one year old to be juveniles. Although we capped population size at four times its initial value, we did not include any density dependent effects on demographic parameters as this theoretical carrying capacity was approached. We chose to use a density independent approach partly because data on density dependent demographic regulation are lacking

for leopards and similar large felids, and partly because we assumed that South African populations are largely limited by a combination of suitable habitat and persecution, and therefore are unlikely to occur at densities that approach carrying capacity defined by resource limitation (see Caro *et al.* 2009).

Model parameters

We used published demographic information for leopards to parameterize the model. A summary of all model parameters and their sources are given in Appendix 1. We estimated initial population structure to be 30% adult males, 30% adult females, 15% subadult males and females respectively, and 10% juveniles. Each time step we drew fecundity from Poisson distributions with a mean annual litter size per female of 1.41 and calculated the total number of juveniles in a given year by summarizing the fecundity of all females. We drew baseline annual survival probabilities from binomial distributions with averages reflecting age and sex specific survival estimated as 91%, 85%, 82%, 93% and 33% for adult males and females, subadult males and females, and juveniles, respectively (Appendix 1). These values were taken from a recent meta-analysis of leopard survival in southern Africa (Swanepoel *et al.,* in press). Although infanticide has been reported as a major cause of juvenile mortality in one leopard population (Balme *et al.* 2013), there are no data available to quantify the effects of male turnover on such infanticide rates (*e.g.* Swenson *et al.* 1997). Furthermore, infanticidal mortality is included in our juvenile survival estimates (Swanepoel *et al.,* in press). We therefore believe that explicit inclusion of the demographic effects of infanticide in our models will only introduce unquantifiable uncertainty, which will hamper the interpretability of the simulation output. We estimated the number of emigrants out of each province from binomial emigration probabilities set to 47% for subadult males, 14% for subadult females and 5% for adults. We calculated the number of immigrants into a province as the sum of the number of emigrants from each neighbouring province scaled by the proportional length of the land border between each pairs of provinces. For international borders, we calculated an average number of immigrants per km of border within South Africa for the respective province, and multiplied this number by the length of the international border. We assumed equal survival for animals migrating between provinces as for animals remaining within their natal province.

We multiplied leopard densities derived from literature and unpublished sources by spatially explicit probabilities of occurrences derived from a habitat suitability model to calculate realistic ranges of provincial population sizes (Swanepoel *et al.* 2013). Source studies used to estimate these densities are given in Appendix 2. Each study was assigned to a major biome, and to incorporate uncertainty in density estimates we calculated a minimum, median and maximum density for each biome. We multiplied these densities by the pixel specific probability of occurrence from our habitat suitability model to calculate the number of leopards per pixel, and estimated provincial leopard population sizes by summarizing the number of animals for all pixels in each province (Table 1). Estimated minimum, median and maximum densities for each province and biome are given in Appendix 3.

We collected information on leopard harvest and retaliatory killing from provincial nature conservation offices for the period 2000–2010. These data contained the number of trophy hunted animals, legally killed problem animals (Damage Causing Animals, DCA) and illegally killed animals. Based on these data, we estimated the sex ratio of hunted leopards under CITES trophy permits to be 68% males and the age structure to be 95% adults, and the sex and age structure for retaliatory killing (*i.e.* estimated from animals killed under DCA permits) to be 65% males and 72% adults (Appendix 1). Due to low compliance to legislation regarding damage-causing leopards, only a low number of reports are received for DCA permits issued, as well as leopards killed under such permits (Chase-Grey 2011). For example, in the Limpopo province reports were only received for 28% of DCA permits issued. Furthermore, record-keeping capabilities varied among provinces, with only Limpopo and KwaZulu-Natal having adequate records on DCA permits issued. Because of these two issues, the number of reported animals killed under DCA permits in each province was low. Therefore, to estimate how many leopards were killed under DCA permits we also collected the number of DCA permits issued for Limpopo and KwaZulu-Natal from 2005 to 2010 (provinces with adequate DCA data). Harvest and retaliatory killing statistics for the South African provinces are listed in Appendix 4.

We set limits for likely ranges of trophy harvest from zero harvest to four times the maximum

Table 1. The range of leopard population sizes and maximum levels of trophy harvest and retaliatory killing used for the simulations for each South African province.

Province	Population size[a]		Trophy harvest Maximum[b]	Retaliatory mortality Maximum[c]
	Minimum	Maximum		
Limpopo	1682	7168	204	348
Mpumalanga	338	1851	32	169
North West	174	255	40	54
Gauteng	25	31	4	8
Northern Cape	68	262	14	27
Free State	8	26	4	8
KwaZulu-Natal	247	1120	20	118
Western Cape	200	619	32	65
Eastern Cape	71	299	16	33
South Africa	2813	11632	366	826

[a]Minimum and maximum population sizes were calculated by multiplying the lowest and highest recorded density in each major biome by spatially derived explicit probabilities of leopard occurrence derived from a habitat suitability model (Appendix 2, Appendix 3).

[b]Represents four times the maximum recorded trophy harvest per year over the period 2002–2010 (Appendix 4), or for provinces without existing harvest the average proportional harvest based on the provinces with existing harvest. Minimum levels were set to zero for each province.

[c]Represents the maximum number of damage-causing leopards killed or translocated per year over the period 2002–2010 (Appendix 4) and an estimated number of illegally killed leopards. Minimum levels were set to zero for each province.

recorded harvest per year in each province. To set an upper limit to harvest for provinces where no harvest had occurred, we first calculated the maximum recorded proportional harvest based on the median population size from the provinces where harvest had occurred. This value was then multiplied by the median population size of the respective province that had been without harvest. We similarly set the lower limits for likely ranges of retaliatory killing at zero killed animals per year in each province. We set the upper limit of likely ranges of retaliatory killing to the maximum number of issued DCA permits plus an estimated number of illegally killed animals. For provinces where we did not have number of issued permits, we calculated maximum proportional annual number of permits per leopard based on the median population sizes in Limpopo and KwaZulu-Natal (where we did have information on number of issued permits), and multiplied this number by the median population sizes for provinces where we did not have information of number of issued permits.

Estimating the number of illegally killed animals was more challenging because detecting illegal killing of carnivores is difficult (Kaczensky *et al.* 2011). During 2010 an anonymous amnesty was given to farmers in the Eastern Cape if they gave information on the number of leopards killed illegally during the years 2004–2010 (Lindsey *et al.* 2011). We therefore used the amnesty data from Eastern Cape in an attempt to quantify illegal killing of leopards in other provinces. To do this we first calculated the proportion of leopards estimated from the median population size that was illegally killed in the Eastern Cape. This proportion was then multiplied by the median population size in the other provinces. Likely ranges of harvest and retaliatory killing for each province and for South Africa that were used in our simulations are given in (Table 1).

Simulations and data analyses

We generated 1000 parameter combinations by sequentially altering values of harvest, retaliatory killing and population sizes within ranges described above. We ran 100 simulations for each parameter combination, resulting in a total of 100 000 individual simulations. For each simulation, we captured population size after 25 years and coded this population size as extinct if fewer than two animals remained or as having declined if it was below initial population size. We used these binary response codes as response variables in generalized linear models to calculate the probability of extinction and population declines (McCarthy *et al.* 1995; Cross & Beissinger 2001; Dalerum *et al.* 2008). We used initial population size, trophy harvest, retaliatory killing as well as all interaction terms as predictors. The models were fitted with a binomial error structure and with a logit link function. We have not reported any evaluations of the test statistics from our logistic models since statistical inference is dependent on sample size, which in simulated data is arbitrarily determined (*e.g.* number

of simulation runs; McCarthy *et al.* 1995; Dalerum *et al.* 2008). Instead, we have presented standardized odds ratios for each model term as a qualitative approach of evaluating their relative influence on extinction risk and risk of population decline (Kaufman 1996). All population simulations and statistical analyses were conducted using R version 2.15.1 for Linux (http://www.r-project.org).

RESULTS

For most provinces, retaliatory killing had substantially higher odds ratios than trophy harvest, both for extinction risk and risk of population decline (Table 2). This highlights that within the evaluated ranges, variation in retaliatory killing had a more pronounced effect on extinction risk and risk of population decline than variation in trophy harvest. The odds ratios for all interaction terms were close to 1 for most provinces (Table 2), which suggests limited interactive effects between trophy harvest, retaliatory killing and population size. The low odds ratios for the effect of population size on extinction risk highlight the positive effect of population size on population persistence. However, for some provinces, as well as for South Africa as a whole, the odds ratios for the effect of population size on risk of population decline was above 1, which suggests a positive association between population size and risk of decline in these areas.

At low to intermediate levels of retaliatory killing, neither the South African leopard population as a whole nor any of the provinces seem to be under serious extinction risk under the current level of trophy harvest (South Africa: 69 animals per year; Limpopo: 51 animals; Mpumalanga: 7 animals; North West: 7 animals; KwaZulu-Natal: 4 animals; Appendix 4), but extinction risk increased across all harvest levels with increasing rates of retaliatory killing in all but two provinces (Fig. 1). Moreover, both the South African leopard population as well as some provinces, most notably Limpopo, Mpumalanga, KwaZulu-Natal and the Western Cape, showed persistent risks of population decline across all evaluated scenarios (Fig. 2).

DISCUSSION

Our simulations pointed to substantially higher effects of variation in retaliatory killing than of variation in trophy harvest on population persistence. We acknowledge that these results could at least be party caused by the wider ranges of retaliatory killing that we simulated compared to harvest, for which the upper limits generally did not reach critical levels to cause increased risks of extinction or population decline. However, we estimated upper limits of retaliatory killing from empirical data, and we set upper limits of harvest to four times the current harvest levels, which must be regarded as liberate. We therefore argue that our results are empirically relevant, because they highlight that the number of animals killed in retaliatory actions can widely exceed the number of animals killed for recreational harvest. Our study thus conforms to previous concerns about the potential effects of persecution on large carnivore population persistence (Treves & Karanth 2003). However, our results contradict some recent studies that have suggested negative demographic effects of trophy harvest alone (Caro *et al.* 2009; Packer *et al.* 2011), and support suggestions that retaliatory killing may enhance such negative effects (Loveridge *et al.* 2009).

The limited relative effect of trophy harvest on population persistence highlights its potential as a strategy to increase local tolerance for large carnivores by providing sustainable incomes (Lewis & Jackson 2005; Treves 2009). However, hunters need to be actively involved in management plans, landowners need to receive associated benefits, and incomes need to exceed any financial losses associated with the presence of predators for positive effects to occur (Treves & Martin 2011). In our simulations, the demographic impacts of retaliatory killing and trophy harvest were also completely additive. The demographic impacts of trophy harvest could therefore be further minimized if it is designed to be compensatory with respect to the killing of conflict animals, *i.e.* if it is directed towards areas with high potential for conflict, or targeting animals that have been identified to cause conflict (Stein *et al.* 2010).

Our results call for concern regarding the sustainability of the South African leopard population. Although our simulations suggested that the extinction risk of the South African leopard population was negligible within the next 25 years, we found an unequivocal risk of population decline in South Africa as a whole as well as for several provinces. Because of the dramatic effects of retaliatory killing on population persistence, our results highlight that reliable data on legal and illegal retaliatory killing are paramount for our ability to assess the sustainability of any given harvest level. Moreover, our results suggest that control of conflict-related killing may be more effective than restricting the CITES quota for harvested animals. Such

Table 2. Standardized odds ratios indicating the effects of trophy harvest, retaliatory killing and population size as well as their interactions on extinction risk and risk of population decline within 25 years of simulated leopard populations. Odds ratios were derived from binomial models based on binary outcomes from a stochastic population model, and describe the change in odds of extinction or population decline over one standard deviation unit of change in each of the predictors (*i.e.* harvest, retaliatory killing and population size).

	Limpopo	Mpumalanga	North West Province	Gauteng	Northern Cape	Free State	KwaZulu-Natal	Western Cape	Eastern Cape	South Africa
Extinction										
Harvest	1.58	1.10	0.04	0.36	0.97	0.37	1.40	0.97	0.98	4.89
Retaliatory killing	2.99×10^{4}	1.12×10^{5}	20.24	0.01	92.76	0.62	1.72×10^{4}	9.28×10^{1}	1.68×10^{1}	0.11
Population size	8.87×10^{-6}	0.00	0.00	0.02	0.02	2.85×10^{-5}	0.02	0.02	0.01	8.38×10^{-9}
Harvest × Retaliatory killing	1.00	1.00	1.32	7.27×10^{3}	1.08	7.18×10^{2}	0.96	1.08	1.03	1.00
Harvest × Population size	1.00	1.00	1.02	1.04	1.00	1.22	1.00	1.00	1.00	1.00
Retaliatory killing x Population size	1.00	1.00	1.02	1.26	0.99	1.35	1.00	0.99	1.00	1.00
Harvest × Retaliatory killing × Population size	1.00	1.00	1.00	0.99	1.00	0.85	1.00	1.00	1.00	1.00
Decline										
Harvest	1.00	1.00	2.27	1.19	1.18	1.89	1.00	1.00	1.00	6.24
Retaliatory killing	1.00	1.00	2.66×10^{3}	6.28×10^{1}	6.30×10^{2}	2.23	1.00	1.00	1.00	1.00×10^{9}
Population size	1.00	1.00	0.05	0.07	0.72	0.01	1.00	1.00	1.00	3.33
Harvest × Retaliatory killing	1.00	1.00	0.83	0.02	0.74	0.04	1.00	1.00	1.00	0.98
Harvest × Population size	1.00	1.00	1.00	1.00	1.00	0.93	1.00	1.00	1.00	1.00
Retaliatory killing × Population size	1.00	1.00	0.98	0.91	0.99	1.09	1.00	1.00	1.00	1.00
Harvest × Retaliatory killing × Population size	1.00	1.00	1.00	1.00	1.00	1.04	1.00	1.00	1.00	1.00

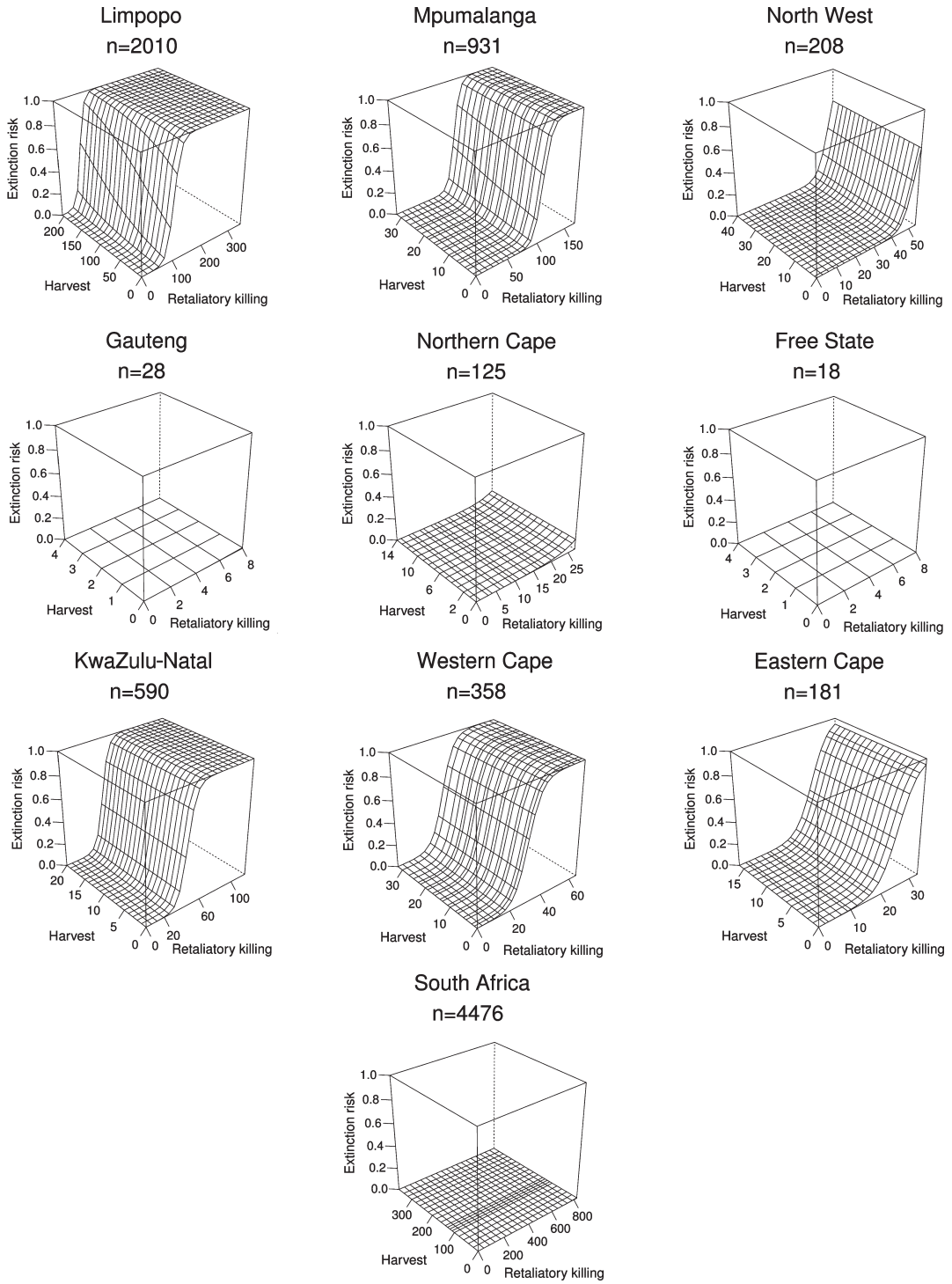

Fig. 1. Predicted extinction risk after 25 years of simulations of provincial leopard populations in South Africa under realistic ranges of trophy harvest and retaliatory killing. Extinction risks were calculated from logistic regression models based on binary outcomes from a stochastic population model. Extinction risks were calculated on the median estimated population estimates within each province, which are indicated in the figure.

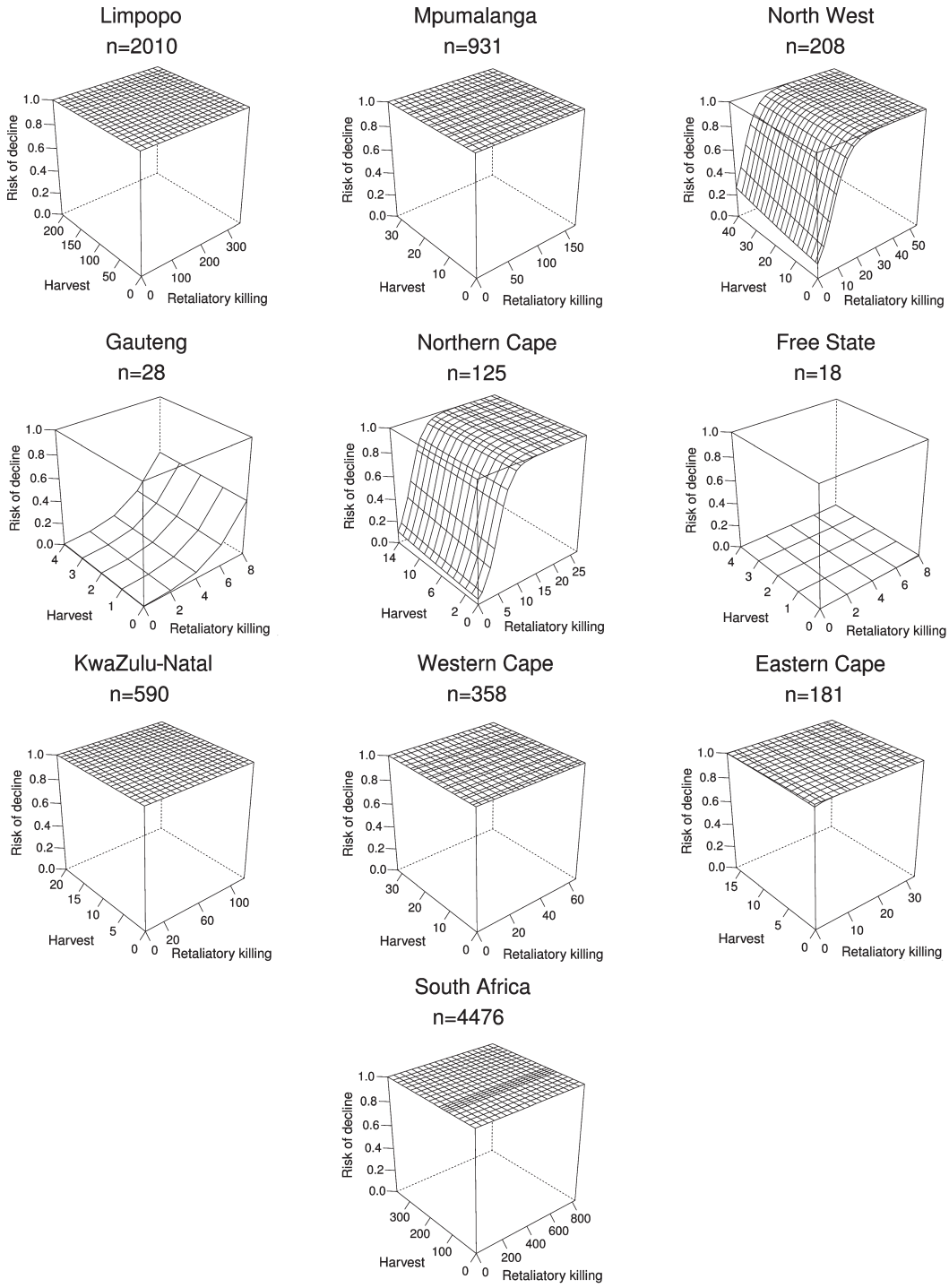

Fig. 2. Predicted risk of population decline after 25 years of simulations of provincial leopard populations in South Africa under realistic ranges of trophy harvest and retaliatory killing. Risks of decline were calculated from logistic regression models based on binary outcomes from a stochastic population model, where a decline was scored if the population size after 25 years of simulation was lower than the initial population size. Risks of decline were calculated based on the median estimated population estimates within each province, which are indicated in the figure.

conflict mitigation could for instance include the use of livestock protection schemes such as livestock-guarding dogs (Ogada *et al.* 2003), but also educational components targeting wildlife associated value norms within local communities (Madden 2004). Adequate and functional compensatory programmes have also been shown effective (Swenson & Andrén 2005), but are highly costly alternatives for financially developing countries.

Some provincial populations experienced high probabilities of decline without experiencing either harvest or retaliatory killing. Since these provinces all had large estimated population sizes, we suggest two, not necessarily mutually exclusive, explanations. First, we parameterized emigration as a proportion of population size, and calculated immigration as the sum of the emigrants from neighbouring provinces. Therefore, provinces with large populations that were surrounded by much smaller ones could experience a net deficit in animals caused by a net emigration that could be enough to cause high risks of population declines. Second, our median population size estimates could be above the demographically stable population sizes given our demographic parameters, so that the observed declines could be the results of a demographic stabilization process. However, our median estimated population size for South Africa (4476 leopards) falls well below the only previous formal attempt to estimate the South African population size (23 472 individuals; Martin & de Meulenaar 1988), and generally agrees with estimates based on expert opinion (*e.g.* 2000–3000 animals: Norton 1990, and 4250 animals: Daly *et al.* 2005). We therefore suggest that factors other than overestimated population sizes caused the elevated probabilities of decline at zero harvest and retaliatory killing in these provinces. We note that three of these provinces, Limpopo, Mpumalanga and KwaZulu-Natal, currently have leopard harvest, which could call for caution in setting harvest quotas for these areas.

Finally, we identify some caveats with our simulation efforts. First, our simulations were based on limited demographic data, including only South African studies (Bailey 2005; Balme *et al.* 2010). We also indirectly estimated leopard population sizes from a habitat suitability model (VanDerWal *et al.* 2009; but see Swanepoel *et al.* 2013), which could have overestimated population size since leopard density estimates were biased towards protected areas. However, we regard our population estimates to be good alternatives to expert opinion estimates, which were our only other option, and our estimates generally agree with such estimates (Norton 1990; Daly *et al.* 2005). Second, our model did not include indirect effect of harvest, for instance related to infanticide (Creel & Rotella 2010). Although such behaviour has been suggested to influence the demographic impacts of harvest both in leopards (Packer *et al.* 2009; Balme *et al.* 2013) and in other large carnivore species (*e.g.* black bears, *Ursus americanus*: Lecount 1987, brown bears, *Ursus arctos*: Swenson *et al.* 1997, and lions, *Panthera leo*: Whitman *et al.* 2004), there are no data available on how male turnover influence such infanticide rates in leopards. Since infanticidal mortality is already included in our model through the survival estimates, we do not believe that explicit incorporation of infanticidal effects in our model would render any improvements in our interpretations. Moreover, although we recognize that our models may have underestimated the influence of male biased killing (*i.e.* harvest), the relative strength of retaliatory killing *versus* harvest suggests that the inclusion of social processes in our models likely would not have change the qualitative outcome of our simulations.

To conclude, our study suggests that control of legal and illegal killing related to human–carnivore conflict may be more effective in promoting the persistence of large carnivore populations than setting restricted trophy harvest quotas. Because we found limited effects of variation in harvest on population persistence, trophy harvest could be one potential avenue for such conflict mitigation. Our study further highlights the necessity for accurate estimates of legal and illegal retaliatory killing for any reliable assessment of sustainable harvest levels. Although our simulations suggested low extinction risk for the South African leopard population within the next 25 years, they indicated very high probabilities of population decline. Our study therefore calls for concern regarding the long-term viability of the South African leopard population. However, because of the large effects of retaliatory killing compared to harvest, we suggest that actions directed to decrease conflict-related killing of leopards may be more effective than restricting trophy harvest in securing the long-term viability of South African leopards.

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APPENDIX 1. Parameters used for modelling the effects of leopard harvest on the probability of population decline and probability of extinction in South African leopard population. Fecundity, survival and dispersal were in the simulations regarded as Poisson and binomially distributed, respectively. Therefore, the variances of these estimates were regarded to be equal to the mean. Age and sex structure of harvest and retaliatory killing were kept as fixed throughout all simulations, to enhance the focus on variability in harvest and retaliatory killing *per se*.

Parameter	Value
Fecundity[a]	1.41
Survival	
adult male[b]	0.91
adult female[b]	0.85
subadult male[b]	0.82
subadult female[b]	0.91
juveniles[b]	0.33
Dispersal[c]	
subadult males	47%
subadult females	14%
adults	5%
Trophy harvest[d]	
age structure	95%
sex ratio	68%
Damage-causing animals[e]	
age structure	72%
sex ratio	65%

[a]Median from Bailey (2005), Owen (2006), Martin & de Meulenaar (1988), Balme *et al.* (2009; 2010), expressed as number of offspring per female per year.

[b]Survival based on protected area estimates from the meta-analysis in Swanepoel *et al.* (in press).

[c]Subadult dispersal based on 36 collared subadults taken from Bailey (2005), Balme *et al.* (2010), Bothma *et al.* (1997), Owen (2006), Stander *et al.* (1997), expressed as percentage animals dispersing per year.

[d]Data on demographic structure of trophy harvested animals collected from Conservation offices based on hunter return forms in Limpopo Province, South Africa, $n = 47$. Age structure is expressed as percentage adults and sex ratio as percentage males.

[e]Data on demographic structure of destroyed problem leopards in Limpopo Province ($n = 21$) and Cape Province (currently Eastern Cape Province, Western Cape Province and Northern Cape Province) ($n = 37$). Data from Limpopo Province were collected directly from conservation offices and data from the Cape Province data taken from C, Stuart and T, Stuart, unpubl. data. Age structure is expressed as percentage adults and sex ratio as percentage males.

APPENDIX 2. Leopard densities (no./100 km²) in each provincial biome that was used to estimate leopard population size in South Africa.

Study no.	Province	Biome/bioregion	Study site	Density	Method	Year	Source
1	Mpumalanga	Lowveld	Southern Kruger National Park	15.63	1[a]	1972	Bailey (2005)
2	Mpumalanga	Lowveld	Central Kruger National Park	15.4	1	1972	Bailey (2005)
3	Mpumalanga	Lowveld	Central Kruger National Park	4.25	1	1972	Bailey (2005)
4	Mpumalanga	Lowveld	Southern Kruger National Park	3.01	1	1972	Bailey (2005)
5	Limpopo (Botswana)	Lowveld	Tuli Game Reserve	8	2[b]	2005–2006	Steyn (2008)
6	Limpopo	Lowveld	Northern Kruger National Park	6.33	1	1972	Bailey (2005)
7	Limpopo	Bushveld	Soutpansberg	19.97	2	2008	Chase-Grey (2011)
8	Limpopo	Bushveld	Welgevonden Game Reserve	4.33	2	2008–2010	L. H Swanepoel, unpubl.
9	Limpopo	Bushveld	Waterberg Biosphere farms	3.18	2	2009	L. H Swanepoel, unpubl.
10	Limpopo	Bushveld	Lapalala Wilderness	3.05	2	2008–2010	L. H Swanepoel, unpubl.
11	KwaZulu-Natal	Lowveld	Mkuze National Park	11.11	2	2005	Balme *et al.* (2010)
12	KwaZulu-Natall	Lowveld	Phinda Private Game Reserve	7.51	2	2005	Balme *et al.* (2010)
13	KwaZulu-Natal	Lowveld	Zululand Rhino Reserve	4.2	2	2006	Chapman & Balme (2010)
14	KwaZulu-Natal	Lowveld	Game farm area in KZN-Natal	2.49	2	2005	Balme *et al.* (2010)
15	North West	Bushveld	Madikwe Nature Reserve	3.86	3[c]	2003	H.L.P. Kelly, unpubl.
16	North West	Bushveld	Pilansberg Nature Reserve	3.45	4[d]	2007	Hayward *et al.* (2007)
17	Western Cape	Fynbos	Cederberg Mountains	2.3	5[e]	2004–2007	Martins (2010)
18	Western Cape	Fynbos	Cederberg Mountains	1.8	5	2004–2007	Martins (2010)
19	Western Cape	Fynbos	Cederberg Mountains	0.8	3	1985	Norton & Lawson (1985)
20	Western Cape	Karoo	Cederberg Mountains	0.9	5	2004–2007	Martins (2010)
21	Western Cape	Karoo	Cederberg Mountains	0.25	5	2004–2007	Martins (2010)
22	Eastern Cape	Fynbos	Baviaanskloof	1.3	5	2007	McManus (2009)
23	Eastern Cape	Fynbos	Baviaanskloof	0.3	5	2007	McManus (2009)
24	Eastern Cape	Lowveld	Baviaanskloof	1.3	5	2007	McManus (2009)
25	Eastern Cape	Lowveld	Baviaanskloof	0.3	5	2007	McManus (2009)
26	Northern Cape	Kalahari	Kgalagadi National park	0.62	5	1984	Bothma & Le Riche (1984)
27	Northern Cape	Karoo	Orange River Basin	0.35	6[f]	1988	C. Stuart & T. Stuart, unpubl.

[a]Method 1; leopard density was estimated by using home range overlap and prey density.
[b]Method 2, leopard density was estimated by applying mark recapture frame work to camera trapping data.
[c]Method 3, leopard density was estimated by using home range analysis and overlap.
[d]Method 4, leopard density was estimated by making predictions on prey density and prey preferences.
[e]Method 5, leopard density was estimated with GPS collar home range data.
[f]Method 6, leopard density was estimated by using sign survey data.

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APPENDIX 3. Minimum, median and maximum leopard densities used in each provincial biome to calculate leopard population sizes in each South African province.

Province	Biome/bioregion	Density (leopards/100km²)		
		Minimum	Median	Maximum
Mpumalanga[a]	Lowveld	3.01	9.80	15.63
Mpumalanga[b]	Bushveld	3.05	3.76	19.97
Mpumalanga[c]	Grassland[d]	0.25	0.60	0.90
Limpopo[e]	Lowveld	6.33	7.20	15.60
Limpopo[f]	Bushveld	3.01	3.76	19.97
KwaZulu Natal[g]	Lowveld	2.49	5.86	11.21
KwaZulu Natal[c]	Grassland [d]	0.25	0.60	0.90
North West[h]	Bushveld[i]	3.45	3.66	3.86
North West[j]	Kalahari	0.31	0.62	1.24
North West[c]	Grassland[d]	0.25	0.60	0.90
Gauteng[h]	Bushveld[i]	3.45	3.66	3.86
Gauteng[c]	Grassland[d]	0.25	0.60	0.90
Free State[h]	Bushveld[i]	3.45	3.66	3.86
Free State[c]	Grassland[d]	0.25	0.60	0.90
Free State[c]	Karoo	0.25	0.60	0.90
Northern Cape[k]	Fynbos[l]	0.80	1.30	2.30
Northern Cape[j]	Kalahari	0.30	0.62	1.24
Northern Cape[c]	Karoo	0.25	0.60	0.90
Western Cape[k]	Fynbos[l]	0.80	1.30	2.30
Western Cape[c]	Karoo	0.25	0.60	0.90
Eastern Cape[m]	Fynbos	0.30	0.80	1.30
Eastern Cape[m]	Lowveld	0.30	0.80	1.30
Eastern Cape[c]	Karoo	0.25	0.60	0.90
Eastern Cape[c]	Grassland[d]	0.25	0.60	0.90

Study numbers below taken from literature sources outlined in Appendix 2.

[a]Min taken from study 4, median calculated from studies 1–4, and max taken from study 1.

[b]Min taken from study 10, median calculated from studies 7–10, and max taken from study 7.

[c]Min taken from study 21, median calculated from studies 20, 21, 27, and max taken from study 20.

[d]We assumed equal leopard densities in the Grassland biome as in the Karroo biome in all provinces.

[e]Min taken from study 6, median calculated from studies 5–6, and max taken from study 5.

[f]Min taken from study 10, median calculated from studies 7–10, and max taken from study 7.

[g]Min taken from study 14, median calculated from studies 11–14, and max taken from study 11.

[h]Min taken from study 16, median calculated from studies 15–16, and max taken from study 15.

[i]We assumed equal leopard densities in the North West, Free State and Gauteng provinces in the bushveld biomes.

[j]Min calculated as half density from 26, median taken from study 26, and max calculated as the double density from study 26.

[k]Min taken from study 19, median calculated from studies 17,18,19, 22, 23, and max taken from study 17.

[l]We assumed equal leopard densities in Northern Cape and Western Cape provinces in the Fynbos biome.

[m]Min taken from study 23, median calculated from studies 22,23,24,25, and max taken from study 22.

Since we did not have estimated leopard densities for all biomes or provinces, we assumed equal leopard densities in the karoo and grasveld biome in all provinces, equal densities in the bushveld biome in the North West, Free State and Gauteng provinces, and equal densities for the fynbos biome in the Northern Cape and Western Cape. For the Kalahari biome, which only had one density estimate, we used half the estimated density as the minimum and double the estimated density as the maximum density.

APPENDIX 4. Number of animals of each sex and age class killed for trophy harvest and under Damage Causing Animal (DCA) permits for each South African province during 2002–2010, as well as number of issued DCA permits in Limpopo (2002–2010) and KwaZulu-Natal (2005–2010).

Year	Age	Harvest			DCA			DCA permits
		Male	Female	Unknown	Male	Female	Unknown	
Limpopo								
2002	Adult	1	0	0	0	0	0	22
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	27	0	0	3	
2003	Adult	4	1	0	1	0	0	13
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	30	0	0	0	
2004	Adult	1	1	0	0	0	0	22
	Subadult	0	0	0	0	1	0	
	Unknown	0	1	30	0	0	0	
2005	Adult	1	1	0	0	0	0	17
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	12	0	0	1	
2006	Adult	4	2	0	0	0	0	21
	Subadult	1	0	0	0	0	0	
	Unknown	0	0	9	0	0	1	
2007	Adult	6	2	0	0	0	0	46
	Subadult	1	0	0	0	0	0	
	Unknown	0	0	13	0	0	2	
2008	Adult	2	0	0	1	0	0	66
	Subadult	0	0	0	0	0		
	Unknown	0	0	47	0	0	65	
2009	Adult	0	0	0	0	0	0	56
	Subadult	0	0	0	0	0	1	
	Unknown	0	0	65	0	0	57	
2010	Adult	10	5	0	0	0	0	63
	Subadult	0	1	0	0	0	0	
	Unknown	1	0	34	0	0	0	
Mpumalanga								
2002	Adult	4	2	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2003	Adult	3	3	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2004	Adult	5	2	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	1	0	0	0	
2005	Adult	4	3	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2006	Adult	4	2	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2007	Adult	6	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	

Continued on p. 130

Year	Age	Harvest			DCA			DCA permits
		Male	Female	Unknown	Male	Female	Unknown	
	Unknown	0	0	0	0	0	0	
2008	Adult	5	2	2	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	1	
2009	Adult	2	2	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2010	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	7	0	0	0	
North West								
2002	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2003	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	19	0	0	0	
2004	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	17	0	0	0	
2005	Adult	7	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2006	Adult	11	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2007	Adult	3	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	2	0	0	0	
2008	Adult	8	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2009	Adult	8	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	2	0	0	0	
2010	Adult	4	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	3	0	0	0	
Gauteng								
2002	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	1	0	0	0	
2003	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2004	Adult	1	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	

Continued on p. 131

Year	Age	Harvest			DCA			DCA permits
		Male	Female	Unknown	Male	Female	Unknown	
2005	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	2	0	0	0	
2006	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2007	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2008	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2009	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2010	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
Northern Cape								
2002	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2003	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2004	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2005	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2006	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	1	
2007	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	1	
2008	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	3	
2009	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	1	
2010	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
Free State								
2002	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	

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Year	Age	Harvest			DCA			DCA permits
		Male	Female	Unknown	Male	Female	Unknown	
	Unknown	0	0	0	0	0	0	
2003	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2004	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2005	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2006	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2007	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2008	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2009	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2010	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
KwaZulu-Natal								
2002	Adult	1	1	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2003	Adult	1	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2004	Adult	1	1	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2005	Adult	1	1	0	0	0	0	7
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2006	Adult	1	0	0	2	0	0	2
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	2	
2007	Adult	0	1	0	0	0	0	5
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2008	Adult	1	1	0	1	0	0	4
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2009	Adult	5	0	0	1	0	0	8

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Year	Age	Harvest			DCA			DCA permits
		Male	Female	Unknown	Male	Female	Unknown	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2010	Adult	5	0	0	1	0	0	8
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
Western Cape								
1977	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	2	4	0	
1978	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	9	4	0	
1979	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	9	1	0	
1980	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	5	10	0	
2002	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2003	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2004	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2005	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2006	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2007	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2008	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2009	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2010	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
Eastern Cape								
2002	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	

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Year	Age	Harvest			DCA			DCA permits
		Male	Female	Unknown	Male	Female	Unknown	
2003	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2004	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2005	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2006	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2007	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2008	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2009	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	
2010	Adult	0	0	0	0	0	0	
	Subadult	0	0	0	0	0	0	
	Unknown	0	0	0	0	0	0	