WILLIAM-GEORGES CROSMARY

LA CHASSE AUX TROPHÉES: CONSÉQUENCES COMPORTEMENTALES, DÉMOGRAPHIQUES, ET ÉVOLUTIVES CHEZ LES POPULATIONS D'ONGULÉS

L'exemple des ongulés des savanes africaines

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RÉSUMÉ

La chasse aux trophées peut contraindre les ongulés à ajuster leur comportement pour réduire le risque de mortalité. De plus, comme cette chasse est basée sur des critères de taille, et biaisée en faveur des mâles, elle peut causer des changements morphologiques vers des individus plus petits, et altérer la structure et la dynamique des populations. La chasse aux trophées est l'un des modes de conservation des habitats naturels. Son potentiel de conservation est encore incertain parce qu'il y a peu d'études en dehors des parcs nationaux, notamment en Afrique. Cette thèse examine les effets de cette chasse sur les ongulés africains, i.e. sur leur comportement, la longueur des cornes, la proportion de mâles adultes, la taille de groupe, et la densité des populations. J'ai travaillé à partir d'observations comportementales et de données populationnelles de suivis à long terme. Pour plusieurs espèces (surtout l'impala *Aepyceros melampus*, le grand koudou *Tragelaphus strepsiceros*, et l'hippotrague noir *Hippotragus niger*), j'ai comparé le comportement, la structure et la densité des populations entre le Parc National de Hwange et les zones de chasse adjacentes, Zimbabwe. Dans les zones de chasse, j'ai analysé les tendances de longueur des cornes au cours des 30 dernières années. Les ongulés venaient davantage de nuit aux points d'eau, et étaient plus vigilants dans les zones de chasse que dans le parc national. L'amplitude de ces ajustements en revanche, était limitée par le besoin en eau, et par le risque de prédation naturelle. La longueur des cornes a décliné, plus particulièrement pour les espèces prisées des chasseurs et subissant une pression de chasse élevée. Il n'y avait pas de différence significative de la proportion de mâles adultes, ou de la taille de groupe, entre les populations du parc national et des zones de chasse. Au cours des 30 dernières années, les densités de population ont globalement davantage diminué dans le parc national que dans les zones de chasse. Ceci suggère que la chasse aux trophées n'a eu qu'un effet minime sur les densités de population par rapport à d'autres facteurs comme les précipitations, ou possiblement la prédation naturelle et l'éléphant. Malgré les ajustements comportementaux, le déclin de la longueur des cornes, et le prélèvement biaisé en faveur des mâles adultes, les densités d'ongulés étaient aussi élevées dans les zones de chasse que dans le Parc National de Hwange. Cette étude illustre comment les zones de chasse aux trophées, lorsque rigoureusement gérées, peuvent jouer un rôle dans la conservation des ongulés africains.

ABSTRACT

Like predation, trophy hunting may constrain ungulates to adjust their behaviour to decrease mortality risk. Moreover, because this removal is size selective and male-biased, it may induce morphological changes towards individuals with smaller traits, alter population structure and dynamics. Trophy hunting is one of the conservation modes of natural habitats, particularly in Africa. However, its conservation potential is still unclear because there are few studies outside National Parks. This thesis aimed to investigate the subtle effects of trophy hunting on African ungulates, i.e. on their behaviour, horn length of harvested males, proportion of adult males, group size, and population densities. I worked from behavioural observations, and from population data of long-term surveys. For several species (mainly impala *Aepyceros melampus*, greater kudu *Tragelaphus strepsiceros*, and sable antelope *Hippotragus niger*), I compared behaviour, population structure, and densities between Hwange National Park and adjacent hunting areas, Zimbabwe. In hunting areas, I analysed trends in horn length of harvested males over the past 30 years. This thesis shows that ungulates drank more often at night, and were more vigilant in hunting areas than in the national park. However, the amplitude of these adjustments was constrained by the need of surface water, and by natural predation risk. Trophy hunting caused a decline in horn length, particularly for species that experienced high hunting pressure and were of high value for hunters. Trophy hunting tended to decrease proportion of adult males, though not significantly, and did not affect group size. Moreover, during the last 30 years, ungulate densities generally declined more in the national park than in neighbouring hunting areas. This suggests that trophy hunting played a minor role on densities compared to other factors, i.e. rainfall, and possibly natural predation and elephant densities. Despite behavioural adjustments induced by hunting risk, decline of horn length, and harvest skewed towards adult males, ungulate densities in hunting areas adjacent to Hwange National Park remained comparable to densities within the national park. This study illustrates how trophy hunting areas, when rigorously managed, may play a significant role in the conservation of ungulates in Africa.

AVANT-PROPOS

Ma thèse est composée de deux sections, comprenant cinq chapitres écrits en anglais sous la forme d'articles scientifiques. J'ai mené la planification, l'acquisition, l'analyse, l'interprétation des données de chacun de ces articles, et en suis l'auteur principal. Mais cette thèse est le fruit d'une riche collaboration entre plusieurs organismes, et divers auteurs y ont donc contribué. Mes deux directeurs de thèse tout d'abord, dans le cadre de ma cotutelle Université Claude Bernard Lyon 1 (France) / Université Laval (Canada): Hervé Fritz, directeur de recherche UMR CNRS 5558 – Laboratoire de Biométrie et Biologie Evolutive de Lyon, et Steeve Côté, professeur titulaire au département de biologie de l'Université Laval. Tous deux sont co-auteurs de tous les chapitres pour leur implication dans le financement et la planification du projet, en plus de la supervision lors de la rédaction et de la révision des manuscrits. Ma thèse s'inscrit dans le contexte du programme de recherche HERD (*Hwange Environmental Research for Development*), collaboration entre le CNRS (Centre National de Recherche Scientifique), le CIRAD (Centre International de Recherche en Agronomie pour le Développement), et la ZNPWMA (*Zimbabwe National Parks and Wildife Management Authority*).

La première partie de ma thèse cherche à voir si le risque de chasse induit des ajustements comportementaux chez les ongulés africains, et si l'amplitude de ces ajustements varie en fonction des espèces, selon leur besoin en eau de surface et leur vulnérabilité aux prédateurs naturels. Cette section comprend le ***Chapitre 2***, écrit en collaboration avec Marion Valeix, alors post doctorante au WildCRU de l'Université d'Oxford, Angleterre, et Hillary Madzikanda, chef écologiste à la ZNPWMA. Tous deux ont été impliqués dans la révision du manuscrit. Ce chapitre intitulé « *AFRICAN UNGULATES AND THEIR DRINKING PROBLEMS: HUNTING AND PREDATION RISKS CONSTRAIN ACCESS TO WATER* » est publié dans le journal *ANIMAL BEHAVIOUR* en 2012. J'y montre que les groupes d'ongulés en zone de chasse basculent partiellement leurs visites aux points d'eau à la nuit, en réponse au risque de chasse diurne, alors que les groupes dans le parc national viennent quasi exclusivement de jour aux points d'eau. Le ***Chapitre 3*** a été écrit en collaboration avec Peter Makumbe, alors étudiant de la *National University of Science and Technology* à Bulawayo, Zimbabwe. Peter Makumbe a participé à la collecte des données, et à la révision du manuscrit. Ce chapitre intitulé « *VULNERABILITY TO PREDATION AND WATER CONSTRAINTS LIMIT BEHAVIOURAL ADJUSTMENTS OF UNGULATES IN RESPONSE TO HUNTING RISK* » sous presse dans le journal *ANIMAL BEHAVIOUR*. Dans le ***Chapitre 3***, je montre que les individus des groupes en zones de chasse passent plus de temps en vigilance que ceux des groupes du parc national, et que les groupes en zones de chasse passent globalement moins de temps autour des points d'eau que les groupes du parc national. Dans les ***Chapitres 2 et 3***, je montre aussi que l'amplitude des ajustements comportementaux en réponse au risque de chasse est limitée, et varie avec l'espèce selon sa contrainte à l'eau de surface et sa vulnérabilité aux prédateurs naturels.

La seconde partie de ma thèse s'intéresse aux effets de la chasse aux trophées à l'échelle des populations, en particulier sur les tendances temporelles et spatiales de la longueur des cornes, et sur les densités de population. Cette partie cherche aussi à évaluer le potentiel de conservation des zones de chasse aux trophées, en comparant l'état de leurs populations d'ongulés avec celui du parc national adjacent. Le ***Chapitre 4*** intitulé « *TROPHY HUNTING IN AFRICA: LONG-TERM TRENDS IN ANTELOPE HORN SIZE* » est soumis à la revue *ECOLOGICAL APPLICATIONS*. Ce chapitre a été écrit en collaboration avec plusieurs coauteurs. Andrew Loveridge du WildCRU a participé à la saisie des données historiques et à la révision du manuscrit. Henry Ndaimani et Vernon Booth, respectivement actuel et ancien écologistes de la station de recherche de Matetsi à la ZNPWMA, ont été en charge de la collecte des données sur le terrain, et ont participé à la révision du manuscrit. Sébastien Lebel, alors représentant du CIRAD au Zimbabwe, a facilité la campagne de saisie des données historiques de terrain, via un financement du CIRAD et de l'ambassade de France au Zimbabwe. Ce chapitre est le premier exemple de tendances temporelles à long terme de la longueur des cornes dans les populations d'ongulés africains chassées pour les trophées. Le ***Chapitre 5*** intitulé « *THIRTY YEARS OF TROPHY HUNTING DID NOT AFFECT POPULATION DENSITIES OF LARGE AFRICAN HERBIVORES IN MATETSI SAFARI AREA, ZIMBABWE* » compare la proportion de mâles adultes, la taille de groupe, et les densités de population d'ongulés dans les zones de chasse *versus* le parc national. Je vise une soumission dans le journal *BIOLOGICAL CONSERVATION* ou *ANIMAL CONSERVATION*. Le ***Chapitre 6*** intitulé « *HUMAN-ELEPHANT INTERFERENCE MAY PROMOTE DENSITIES OF A RARE ANTELOPE IN ELEPHANT-DOMINATED AFRICAN SAVANNAS* » a été écrit en collaboration avec Simon Chamaillé-

Jammes, chercheur permanent à l'UMR 5175 – Centre d'écologie fonctionnelle et évolutive (CEFE), qui a participé à la révision du manuscrit. Godfrey Mtare, alors écologiste du bloc de Main Camp dans le Parc National de Hwange, a participé à la collecte de données. Ce chapitre compare les densités d'hippotragues noirs le long d'un gradient de perturbation humaine dans l'écosystème de Hwange, et montre que ces densités sont étonnamment plus élevées à l'extérieur du parc national. Nous y discutons le rôle qu'a peut-être joué l'éléphant dans ce résultat surprenant. Ce chapitre est en révision dans le journal *BIODIVERSITY AND CONSERVATION*.

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Vient le temps des mercis, des bises et des clins d'œil… Pour moi, c'est l'occasion de dire que j'ai vécu ce doctorat comme une belle aventure humaine. Un (pas assez) long et (très) excitant terrain en Afrique, une (souvent trop) longue et (parfois moins) excitante phase d'écriture, entre Québec et France. Périodes propices aux chocs culturels, climatiques, mais surtout aux belles rencontres.

L'Afrique

Merci à **Hervé Fritz**. Au delà du sujet de thèse, tu m'as donné la possibilité de venir vivre mon rêve d'enfant dans la savane, accompagné de ma famille. Cela compte pour moi, et je m'en souviendrai longtemps. J'ai aussi apprécié la liberté que tu m'as laissée tout au long de mon doctorat, que ce soit sur les thèmes abordés, ou sur mon choix d'aller rédiger au Québec. Une grande qualité de ton encadrement est ton intelligence des gens, et bien sûr ta « positive attitude ».

Marion, c'est toi le *starter* dans cette histoire. Je continue de me demander si je dois tout ça aux chocolats que je te ramenais à Chizé lorsque toi-même rédigeais ta thèse. Merci Marionnette de m'avoir confié les clefs du projet!

Simon, je sais que tu l'as eu mauvaise lorsque j'ai dû quitter notre *boys band* mexicain. Il fallait que je tente une carrière en solo. Promis, on reforme l'équipe à Cuba pour l'organisation des tournois féminins de *beach volley*. On avait aussi parlé d'une production de films à Jwapi, non?

Nolwenn, jamais les *hits* des années 80 n'auront eu autant de saveur qu'en ce soir de pleine lune à Jwapi. OK, la bouteille de whisky, et les mégots de Berkeley ont sûrement aidé à sublimer les mélodies de Desireless, et autre Jeanne Mas. Mais quand même, on sait tous deux la profondeur de ces vers: « tes états d'âme Eric, sont comme les états d'Amérique ». A toi mon alter ego mélomane.

Tawanda, thanks to you Hwange proudly hosts the very first graduate sable antelope on human biology. Subject of its study: « Flight distance of a student in response to an approaching sable ». Apparently, some bees have also submitted a thesis on « How many bites can a student undergo before he abandons his field position? ». **Peter**, you're responsible of one of my worst memories during the three years passed in Hwange, you defeated me at Risk! How could have you betrayed me while I was kind enough to let you do so many 24H00 counts and days of data entry… What a thanklessness!

Nico, on ne fera plus de pétanque arrosée au pastaga à Ngweshla, de plongée à Sanary, de luge sur les plaines d'Abraham. Mais on l'a fait! Ce qui est dur à avaler mon Nico, c'est que tu es parti sans m'avouer que c'était toi qui t'étais honteusement bâfré l'assiette de *nachos*! On s'en reparlera.

Maël, un merci pour l'Afrique, un merci pour le Québec, un double merci…un par mamelle quoi.

Hugo, ou le petit plus. Il doit me rester à peu près 10,000 heures sur tes 150 K7 à dépouiller. Je dois même pouvoir y trouver des lions, des guépards, des hippos, et des grues. Je te souhaite d'avoir un assistant aussi compétent et passionné sur ton terrain de thèse.

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Isa et **Gizou**, mes amies du Bacc, co-fondatrices du groupe des…des quoi déjà?

Merci à **Marianne**, et surtout à ses oreilles qui ont souvent chauffé à entendre mes discussions salaces.

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Milán-James et **Perrine**, combien je suis chanceux et heureux de vous avoir! Cette thèse vous est dédiée. *Done*! On part où maintenant?

« *Azur! nos bêtes sont bondées d'un cri! Je m'éveille, songeant au fruit noir de l'Anibe dans sa cupule verruqueuse et tronquée... Ah bien! les crabes ont dévoré tout un arbre à fruits mous. Un autre est plein de cicatrices, ses fleurs poussaient, succulentes, au tronc. Et un autre, on ne peut le toucher de la main, comme on prend à témoin, sans qu'il pleure aussitôt de ces mouches, couleurs!... Les fourmis courent en deux sens. Des femmes rient toutes seules dans les abutilons, ces fleurs jaunes tachées de noir pourpre à la base que l'on emploie dans la diarrhée des bêtes à cornes... Et le sexe sent bon. La sueur s'ouvre un chemin frais. Un homme seul mettrait son nez dans le pli de son bras. Ces rives gonflent, s'écroulent sous des couches d'insectes aux noces saugrenues. La rame a bourgeonné dans la main du rameur. Un chien vivant au bout d'un croc est le meilleur appât pour le requin... - Je m'éveille songeant au fruit noir de l'Anibe; à des fleurs en paquets sous l'aisselle des feuilles.* »

(Saint John Perse, Eloges, V).

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INTRODUCTION GÉNÉRALE

WILLIAM CROSMARY

CHASSE, HISTOIRE ET CONSERVATION

Source de nourriture et d'extinctions

Parmi l'ensemble des activités humaines, et le dérangement qu'elles occasionnent sur les populations animales (Frid et Dill, 2002), la chasse est certainement celle qui suscite le plus de controverse dans le monde de la conservation (Dickson et al., 2009). Elle est intimement liée à l'histoire de l'humanité, et a contribué à son développement, mais bien souvent au détriment des espèces animales exploitées. À la fin du Quaternaire[1], la croissance démographique, l'expansion géographique, ainsi que la sophistication des techniques et outils de chasse de l'Homme moderne *Homo sapiens*, ont précipité les extinctions de grands mammifères en Eurasie, Australie, Amérique, et à Madagascar (Martin et Steadman, 1999; Johnson, 2002). A l'instar du mammouth laineux *Mammuthus columbi*, ou du mastodonte américain *Mammut americanum* (Grayson et Meltzer, 2003), de nombreuses espèces de mégafaune[2] ont disparu au gré des colonisations humaines de nouvelles zones géographiques. Parmi les espèces de gibier ont alors survécu principalement celles qui ont pu trouver refuge face à l'essor anthropique (Surovell et al., 2005). Ainsi la chasse a-t-elle accompagné les hommes dès le début de leur histoire. Plus récemment, au 16ème siècle, avec l'expansion mondiale des empires coloniaux d'Europe, marins, fermiers et pionniers européens ont fait disparaître de nombreuses espèces animales, comme par exemple le dodo *Raphus cucullatus* au 17ème siècle (Roberts et Solow, 2004), ou le grand pingouin *Pinguinus impennis* au 19ème siècle (Fuller, 1999).

Aujourd'hui, la chasse de subsistance est certainement la forme d'exploitation de la faune sauvage la plus menaçante pour la conservation de nombreuses espèces des milieux tropicaux. Dans les régions du monde en développement, cette chasse est souvent la principale source de protéines et d'argent pour les hommes (FAO [Food and Agricultural Organization of the United Nations]/WHO [World Health Organization], 1992a, b; Wilkie et Carpenter, 1999a; Barnes, 2002; Loibooki et al., 2002). Dans les sociétés africaines par exemple, la chasse et le commerce de viande de brousse ont une histoire de plusieurs siècles (Lewicki, 1974). Seulement, depuis le début du 20ème siècle, avec le remarquable

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[1] Il y a entre 100,000 et 10,000 ans.

[2] Mammifères géants pour la plupart.

essor démographique humain[3], la pression anthropique sur les espèces de gibier s'est considérablement accentuée (Barnes, 2002). Cette chasse à la viande de brousse n'est ainsi plus pérenne (Robinson et Bennett, 2000). En effet, aux taux actuels de prélèvement, les populations animales diminuent rapidement, et disparaissent même par endroits (Redford, 1992; Rabinowitz, 1998; Maisels et al., 2001). Dans les forêts tropicales d'Afrique Centrale par exemple, l'exploitation de la faune est actuellement six fois supérieure au taux d'exploitation durable (Bennett, 2002). Ceci signifie que l'apport protéique par la chasse de subsistance va considérablement diminuer dans le futur (Fa et al., 2003), tout comme les populations de moyens et de grands mammifères (Fa et al., 2002), principales pourvoyeuses de viande de brousse. De plus, cette situation est aggravée par la dégradation et la disparition des habitats naturels.

L'exploitation de la vie sauvage par l'humain a donc été, et est encore aujourd'hui, un facteur majeur de perte de biodiversité (Diamond, 1989). La surchasse est la principale responsable de la plupart des extinctions récentes (Caughley et Gunn, 1995), et elle menace encore aujourd'hui beaucoup d'espèces dans le monde (IUCN, 2007). Un tiers des espèces de mammifères et d'oiseaux menacées d'extinction continue en effet de décliner du fait de la surexploitation par l'homme (Hilton-Taylor, 2000). La situation est particulièrement préoccupante pour les espèces de grands herbivores (i.e. masse corporelle >5kg; revue dans Fritz et Loison, 2006). Tout d'abord parce qu'elles représentent une part importante des espèces chassées, et sont sources de nourriture et d'argent pour de nombreuses populations humaines (Milner-Gulland et al., 2003a). Ensuite parce qu'elles sont la pierre angulaire des écosystèmes terrestres, influençant leur structure, leur composition, et leur fonctionnement (McNaughton et Georgiadis, 1986; Collins et al., 1998). La gestion et la conservation des grands herbivores sont donc essentielles pour des considérations écologiques et socio-économiques (Gordon et al., 2004).

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[3] La population humaine d'Afrique sub-saharienne est passée de 84 millions en 1900, à 168 millions en 1950 et à 612 millions en 2000 (McEvedy and Jones, 1978; United Nations, 2000).

Chasse sportive et « bouchers pénitents »

Outre le fait qu'elle répond à un besoin alimentaire, la chasse se pratique aussi pour des motivations culturelles (McCorquodale, 1997), pour limiter les populations animales surabondantes et nuisibles aux activités humaines (Côté et al., 2004), et comme activité récréative (Dickson et al., 2009). Ce dernier type de chasse, dit aussi chasse sportive, a pour principal objectif de divertir le chasseur. La chasse sportive a une longue histoire. Elle était déjà pratiquée dans l'Egypte ancienne des pharaons, dans les grandes seigneuries d'Europe du Moyen-Age, dans les colonies des empires européens des derniers siècles, et l'est encore aujourd'hui à travers le monde. Les safaris africains en sont probablement l'exemple actuel le plus populaire. A l'époque victorienne[4], les célèbres expéditions d'explorateurs britanniques tel Frederik Selous[5], guide des safaris gargantuesques de Théodore Roosevelt, ont fait la légende des safaris de chasse en Afrique. Le récit de ces histoires continue d'exciter l'imaginaire des amateurs de chasse, principalement européens et américains, et de susciter leur engouement pour cette destination cynégétique.

Dans les colonies africaines du 19ème siècle, le rapide succès de la chasse sportive précipite l'extinction d'espèces emblématiques comme le quagga *Equus quagga quagga*, et la quasi extinction d'autres comme le zèbre de montagne du Cap *Equus zebra zebra* (Adams, 2004). Se manifeste alors chez les chasseurs de l'époque, le sentiment d'urgence de préserver ces opportunités de chasse, et se développe l'intérêt pour la conservation de la faune et des habitats naturels (MacKenzie, 1988). Ainsi, dès la fin du 19ème siècle, bon nombre de chasseurs professionnels élèvent leur voix pour stigmatiser une chasse non « *fair-play* », « assoiffée de sang » (Fitter et Scott, 1978), et responsable de la disparition de trop d'espèces. Cet éveil d'une conscience conversationniste chez ces « bouchers pénitents[6] » est à l'origine de la création d'organisations de conservation vers la fin du 19ème siècle, tel que le *Boone and Crockett Club* en Amérique, ou encore la *Society for the Preservation of the Wild Fauna of the Empire*[7] dans l'Afrique victorienne (Prendergast et

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[4] De 1830 à 1900.

[5] Explorateur britannique du 19ème siècle en Afrique de l'Est et Afrique australe.

[6] De l'anglais *penitent butchers*. Termes qui illustrent de manière péjorative les chasseurs qui ont pris conscience de la nécessité de réguler la chasse, seulement une fois rompus et lassés de safaris (Fitter et Scott, 1978).

[7] Aujourd'hui devenue *Fauna & Flora International*. www.fauna-flora.org.

Adams, 2003). Cette dernière travaillait alors comme un groupe de pression visant à influencer la politique coloniale en Afrique. Ses membres étaient des chasseurs, des gouverneurs, des administrateurs des colonies et des protectorats africains, des *leaders* d'autres parties du monde, dont le plus illustre fut certainement Theodore Roosevelt. Ils ont encouragé la mise en place de règlementation et de licences pour la chasse sportive en Afrique australe et en Afrique de l'Est. Ainsi ont-ils établi une liste d'espèces en danger d'extinction, défini des catégories d'individus non chassables (e.g. immatures, femelles gestantes), interdit la vente de trophées trop petits (e.g. minimum de 5kg pour les défenses d'éléphant *Loxodonta africana*), favorisé la création de réserves de chasse pour protéger les habitats naturels de l'empiètement humain, et imposé des quotas de chasse (revue dans Prendergast et Adams, 2003). Ce sont là les prémices des aires protégées et de la régulation de la chasse sportive, deux piliers de la philosophie de la conservation au 20ème siècle (Anderson et Grove, 1987).

Chasser pour mieux conserver

Dans les colonies d'Afrique du début du 20ème siècle, ces « bouchers pénitents » ont imposé une philosophie occidentale de la conservation, au détriment des besoins et des droits ancestraux des populations humaines autochtones. Une pratique de conservation héritée de cette époque est la réquisition de grands espaces naturels (McNaughton, 1989) desquels les installations et activités humaines sont restreintes, voire exclues. Ces aires « strictement » protégées (IUCN catégories I-III *sensu* WRI/UNEP/UNDP/WB, 1996), tel que les parcs nationaux, suscitent l'hostilité des populations humaines locales qui en ont été déplacées et s'y sont vues interdire l'exploitation des ressources (e.g. viande de brousse, bois, pâtures pour troupeaux domestiques). Une hostilité qui est exacerbée par les coûts subis par ces populations en périphérie des aires protégées, i.e. attaques de grands carnivores sur hommes et cheptels (Packer et al., 2005; Holmern et al., 2007), razzias des éléphants sur les cultures (Hoare, 2000), etc. C'est un problème qui s'accentue avec l'expansion démographique humaine et son empiètement sur les habitats naturels (Newmark et al., 1994).

La création et la gestion des aires protégées dites « strictes » requièrent des efforts financiers considérables. Il faut par exemple plus de US$200/km^2 pour protéger l'ivoire des défenses d'éléphants ou les cornes de rhinocéros des braconniers (Leader-Williams et Albon, 1988), sommes que les gouvernements des pays en voie de développement peinent souvent à investir. D'autre part, ces aires protégées « strictes » seules ne sont pas suffisantes pour garantir la conservation de la vie sauvage (revue dans Newmark, 2008). La conservation doit en effet s'étendre à l'extérieur de ces aires protégées, là où résident encore de nombreuses populations animales (Fjeldsa et al., 2004; Western et al., 2009).

Au début du 20ème siècle s'est développée la notion de conservation « utilitaire » (de l'anglais *utilitarian conservation*; Leopold, 1933) selon laquelle la faune, via sa commercialisation, peut et doit contribuer au développement des populations humaines. De cette mouvance, naissent dans les années 1980 en Afrique australe les programmes de conservation basés sur la participation des communautés humaines locales (de l'anglais *Community-Based Natural Resource Management, CBNRM*; revue dans Jones, 2009). L'idée principale de ces programmes est de redonner aux communautés humines locales le droit à l'exploitation de la faune sur leurs terres, et d'ainsi endiguer leur hostilité à l'égard des aires protégées (Hulme et Murphree, 2001). Ces populations bénéficient alors directement de la valeur marchande de la faune en la commercialisant et ont un intérêt substantiel à la conserver (Metcalfe, 1994; Lewis et al., 1990; Muir-Leresche et al., 2003).

Le tourisme de faune, autrement nommé « écotourisme » ou encore « tourisme vert », est le principal mode de commercialisation de la faune dans le monde. Il existe sous deux formes. Le tourisme photographique tout d'abord, forme non consommatrice (de l'anglais *nonconsumptive tourism*) de l'écotourisme, essentiellement pratiqué dans les parcs nationaux et autres aires strictement protégées. Puis la chasse sportive, forme consommatrice (de l'anglais *consumptive*) pratiquée à l'extérieur des aires strictement protégées, dans des aires dites « partialement » protégées (IUCN catégories IV and V *sensu* WRI/UNEP/UNDP/WB, 1996), où peuvent être aussi autorisées d'autres formes d'exploitation des ressources naturelles (e.g. exploitation forestière).

La chasse sportive est aujourd'hui pratiquée dans le monde entier (Lindsey et al., 2007a; Frisina et Tareen, 2009; Sharp et Wollscheid, 2009), et s'avère être parfois un outil de conservation plus pertinent que le tourisme photographique. Par exemple, la chasse sportive requiert moins d'infrastructures touristiques, génère autant d'argent pour des volumes touristiques moindres, et a donc potentiellement moins d’impact sur l’environnement que le tourisme photographique (Chardonnet, 1995; Roe et al., 1997; Leader-Williams, 2000). Elle est d’autre part davantage résiliente à l’instabilité socio-économique et politique de certaines destinations touristiques, et assure donc des revenus continus de devises étrangères dans des pays délaissés par le tourisme photographique (Wilkie et carpenter, 1999b). De plus, un chasseur touristique peut dépenser entre 50,000 et 120,000 dollars américains pour un safari en Afrique. Une partie de cet argent peut être réinvestie dans la gestion des aires protégées (Lewis et Alpert, 1997; Lindsey et al., 2007b) et servir à financer des programmes de conservation et de réintroduction (Leader-Williams et al., 2001, 2005; Flack, 2003; Lindsey et al., 2006).

Pour les propriétaires terriens, entrepreneurs privés, ou populations locales, la chasse sportive représente donc une alternative économique à l’agriculture et à l’élevage, en particulier dans les pays en voie de développement (Bond, 1999). La création de zones de chasse permet ainsi de ralentir l’expansion humaine sur les habitats naturels (Lindsey et al., 2007b) et renforce le réseau d’aires protégées. De plus, disposées en périphérie de ces derniers, les zones de chasse agissent comme des zones tampons réduisant l’effet de bordure dû aux activités humaines en périphérie (Woodroffe et Ginsberg, 1998).

LES EFFETS DE LA CHASSE SPORTIVE SUR LES POPULATIONS EXPLOITÉES

La chasse sportive peut rester un moyen efficace de conservation à la condition que les populations animales soient exploitées durablement, sans risque pour leur conservation. Il faut aussi que le succès de chasse et la présence d’animaux de qualité (i.e. trophées) satisfassent les attentes des chasseurs. Sans ces conditions, les zones de chasse risquent de ne pas être écologiquement et économiquement viables, et par conséquent de ne pas être utiles à la conservation. Traditionnellement, la principale question que se posent les scientifiques et gestionnaires quant aux effets de la chasse s’articule autour de la dynamique des populations exploitées, à savoir combien d’individus peuvent être prélevés dans une population sans que cette dernière ne décline (Caughley, 1977). En comparaison, les répercussions du dérangement provoqué par la chasse sur le comportement animal ont été plus marginalement évoquées (e.g. Kufeld et al., 1988; Benhaiem et al., 2008). Dans un cas comme dans l'autre, ce sont des études d'écosystèmes de l'hémisphère Nord. Or en Europe et en Amérique du Nord, l'expansion humaine des 19ème et 20ème siècles a causé la chute drastique, voire la disparition par endroits, des populations de grands prédateurs (Berger, 1999; Woodroffe, 2000). Ce déclin des grands prédateurs a favorisé l'augmentation des populations de grands herbivores (e.g Andersen et al., 1998; Milner et al., 2006), voire la surabondance de certaines populations qui doivent aujourd'hui être régulées pour préserver l'intégrité des écosystèmes (Côté et al., 2004). Dans ce contexte, l'industrie de la chasse s'est développée avec succès dans ces régions, en partie comme outil de régulation (Festa-Bianchet, 2007). Il n'y a donc pas, en général, de préoccupation majeure de conservation pour les populations de grands herbivores chassées dans ces écosystèmes, même s'il existe des exceptions.

La déclinaison la plus populaire de la chasse sportive est la chasse aux trophées, i.e. chasse aux individus arborant les caractéristiques sexuelles secondaires (e.g. bois, cornes, défenses) les plus proéminentes. Les quotas de la chasse aux trophées ne représentent généralement qu'un faible pourcentage d'individus des populations exploitées, et ne concernent en général que les mâles adultes (Bond et al., 2004). L'effet de ce type de prélèvement sur la dynamique des populations chassées et sur le comportement des individus peut donc à priori être considéré comme minime, voire négligeable. Néanmoins, de plus en plus d'études montrent que les prélèvements sélectifs, sur des considérations de sexe, d'âge, ou de phénotypes, peuvent avoir des répercussions démographiques et évolutives subtiles, i.e. autre que la simple soustraction d'un petit nombre d'individus dans les populations exploitées (revues dans Milner et al., 2007; Allendorf et Hard, 2009).

Effets directs: moins de mâles adultes et trophées de plus en plus petits

A l'instar de la prédation, la chasse affecte directement la dynamique des populations de proies en augmentant la mortalité (Caughley, 1977; Solberg et al., 1999). Mais est-ce vrai pour cette chasse particulière qu'est la chasse aux trophées, puisque les proportions d'individus prélevées sont très faibles et ne concernent qu'une catégorie d'individus, les mâles adultes aux plus grands bois ou cornes?

Moins de mâles adultes… Et alors?

Les populations de grands herbivores sont très structurées en sexe et en âge, avec des taux de survie et de reproduction qui diffèrent selon le sexe et l'âge des individus (Gaillard et al., 1998). Ainsi, des populations de mêmes tailles mais de structures différentes suivent des dynamiques distinctes (Coulson et al., 2001), et risquent donc de répondre différemment aux variations environnementales (Cameron et Benton, 2004).

Le prélèvement biaisé en faveur des mâles dans les populations de grands herbivores est une pratique de gestion commune dans le monde (e.g. Amérique du Nord: McCullough, 2001; Europe: Langvatn et Loison, 1999; Afrique: Ginsberg et Milner-Gulland, 1994). D'une part parce que ce sont les mâles qui arborent les traits physiques recherchés des chasseurs, d'autre part parce que les populations au rapport des sexes biaisé en faveur des femelles sont théoriquement plus productives (Caughley, 1977). Dans les populations où il y a moins de mâles, les femelles bénéficieraient en effet d'une diminution de la compétition et de l'agressivité exercées par ces derniers. Et ce, sans pour autant qu'il y ait déclin du taux de fécondité puisque la reproduction, chez les espèces polygynes tout du moins, n'est en principe pas limitée par le nombre de mâles présents dans la population. De fait, le rôle des mâles dans les modèles de dynamique de population des grands herbivores a traditionnellement été négligé (Gaillard et al., 1998, 2000; mais voir Ginsberg et Milner-Gulland, 1994; Mysterud et al., 2002).

Toutefois, que la fécondité et le recrutement soient résilients, voire positivement corrélés à un rapport des sexes biaisé en faveur des femelles, n'est pas toujours garanti (Solberg et al., 2000). Ainsi, lorsqu'il y a beaucoup moins de mâles adultes que de femelles, la productivité de la population risque de diminuer (Gruver et al., 1984; Ginsberg et Milner-Gulland, 1994). C'est le cas par exemple de la population d'antilope saïga d'Asie Centrale *Saiga tatarica* (1 mâle pour 106 femelles; Milner-Gulland et al., 2003b), ainsi que de certaines populations de wapiti en Amérique du Nord *Cervus elaphus* (5 mâles pour 100 femelles; Noyes et al. 1996). D'autre part, comme la taille des traits sexuels secondaires croît avec l'âge des mâles, les plus gros bois/cornes sont nécessairement arborés par des mâles d'âge mûr. En prélevant ces derniers, les chasseurs biaisent donc le segment mâle de la population vers les jeunes classes d'âge (e.g. Laurian et al., 2000; Sæther et al., 2004).

Lorsque la proportion de mâles adultes diminue, les jeunes mâles sont davantage libres de participer à la reproduction, et augmentent donc leur effort reproducteur (Mysterud et al., 2003; Sæther et al., 2003; Bonenfant et al., 2004). Si la participation de ces jeunes mâles à la reproduction compense parfaitement le manque de mâles adultes est sujet à débat. En effet, les jeunes mâles pourraient recourir à des comportements de cour immatures, susceptibles de réduire la probabilité que les femelles s'accouplent (Squibb, 1985; Shackleton, 1991).

La plus faible proportion de mâles adultes, conjuguée au manque d'expérience des plus jeunes mâles, causeraient un délai dans la fécondation des femelles (Noyes et al., 1996; Singer et Zeigenfuss, 2002). Ceci pourrait aussi par la suite entrainer un délai et de l'asynchronie dans les mises bas (Larkin et al., 2002; Noyes et al., 2002; Holand et al., 2003). Or, la masse et la survie des nouveaux-nés sont très corrélées aux dates et à la synchronie des naissances (Sæther et al., 2003; Holand et al., 2006). Et donc, un délai dans la conception risque de réduire le recrutement dans la population. De même, la date et la masse des jeunes à la naissance déterminent en partie leur masse à l'âge adulte, laquelle influencera leur survie (Guinness et al., 1978; Côté et Festa-Bianchet, 2001) et leur reproduction (Sæther et Heim 1993; Festa-Bianchet et al., 2000), et donc la dynamique de leur population (Gaillard et al., 2000).

Sélection cynégétique et contre sélection évolutive des grands bois/cornes

L'exploitation basée sur des caractéristiques de taille favoriserait les individus qui investissent plus tôt dans la reproduction, au détriment de la croissance et du développement des caractéristiques sexuelles secondaires (Browman, 2000). Les phénotypes sélectionnés par les chasseurs aux trophées, tels que les cornes, bois, et défenses, sont généralement héritables (Williams et al., 1994; Réale et al., 1999; Kruuk et al., 2002; Coltman et al., 2003). Par conséquent, le prélèvement d'individus aux grands trophées peut créer une sélection artificielle en faveur des individus aux trophées plus petits. Les changements phénotypiques dans les populations dont les individus sont prélevés sur des caractéristiques physiques ont été bien documentés chez les poissons (e.g. Sutherland, 1990; Browman, 2000), mais moins chez les grands herbivores chassés pour leurs trophées (Jachmann et al. 1995; Harris et al., 2002; Coltman et al., 2003; Garel et al., 2007). Or, un déclin de la taille des trophées dans ces populations pourrait menacer leur viabilité puisqu'il y a des corrélations génétiques entre la taille des trophées et la valeur adaptative des individus (Hartl et al., 2003; Coltman et al., 2005). D'autre part, un déclin de la taille des trophées dans une zone de chasse risque de rendre cette dernière moins attractive auprès des chasseurs, et met donc en péril son économie, et par conséquent son potentiel de conservation.

La variation de la qualité des trophées n'est pas simplement tributaire de l'effet sélectif de la chasse aux trophées. Les facteurs environnementaux sont eux aussi susceptibles d'influencer les variations temporelles et spatiales de taille de trophées. Les mâles développent en effet de moins grands trophées lorsque les conditions environnementales se dégradent, e.g. phénomènes dépendants de la densité (Jorgenson et al., 1998; Festa-Bianchet et al., 2004; Schmidt et al., 2007), détérioration des habitats favorables (Garel et al., 2007), évènements climatiques extrêmes (i.e. sécheresses; Torres-Porras et al., 2009). De même, la proximité d'une zone protégée (e.g. un parc national) peut théoriquement atténuer l'effet négatif de la chasse sélective sur la taille des trophées, par la dispersion de mâles de la zone protégée dans les zones de chasses avoisinantes (Tenhumberg et al., 2004).

Effets indirects[8]: ajustements comportementaux

Les études comportementales peuvent et doivent être utiles à la biologie de la conservation (Sutherland, 1998; Caro, 2007). Avec de plus en plus de dérangement anthropique sur les habitats naturels, il y a une préoccupation grandissante sur la façon dont changent les comportements des animaux dérangés par les activités humaines (Geist, 1970; Caro, 1999). Se pose en particulier la question de savoir si, et comment, ces perturbations anthropiques, par le truchement des ajustements comportementaux des animaux, peuvent affecter la dynamique des populations exploitées. Longtemps, l'approche démographique a tenu le haut du pavé parmi les études portant sur les conséquences de la chasse sportive.

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[8] Le terme « indirects » fait référence aux effets du dérangement induit par le risque de chasse sur le comportement animal, en opposition aux effets « directs » qui représentent eux les effets du prélèvement de quelques individus. « Indirects » ici ne doit donc pas être compris dans le sens de l'analyse de pistes (*sensu* Shipley, 2009).

Aujourd'hui, de plus en plus d'études comportementales sont menées (e.g. Kufeld et al., 1988; Benhaiem et al., 2008). Et ceci est justifié sachant que la façon dont les proies répondent au risque de prédation est un thème central de l'écologie, largement étudié dans le cadre des relations prédateurs-proies (Lima et Dill, 1990).

La théorie de l'approvisionnement optimal (MacArthur et Pianka, 1966) prédit que le risque de prédation peut contraindre les comportements d'approvisionnement et la distribution spatiale des proies, puisque ces dernières doivent faire un compromis entre leurs besoins en ressources et leur sécurité. À mesure que le risque de prédation augmente, les proies investissent plus de temps et d'énergie dans les comportements d'anti-prédation. La vigilance est l'un des comportements d'anti-prédation le plus souvent mis en exergue dans des études théoriques et empiriques (revue dans Bednekoff et Lima, 1998; Treves, 2000). Lorsque le risque de prédation augmente, les proies sont plus vigilantes, i.e. elles passent plus de temps à surveiller leurs environs. Ce comportement peut leur permettre de détecter suffisamment tôt un danger potentiel (e.g. prédateur qui approche), et réagir en conséquence (e.g. fuite). Bien que les proies bénéficient de ce comportement en réduisant le risque de mortalité, elles ne peuvent pas être continuellement en vigilance. Ce comportement nécessite en effet une attention visuelle quasi exclusive, et est donc adopté au détriment d'autres activités améliorant la valeur sélective des individus, tel que l'approvisionnement en nourriture (e.g. Beauchamp et Livoreil, 1997; Fritz et al., 2002; mais voir Illius et Fitzgibbon, 1994; Fortin et al., 2004). Les proies qui vivent en groupe bénéficient de l'agrégation parce que le risque d'être repéré, et traqué par un prédateur, diminue avec la taille du groupe (« *dillution effect* », Hamilton, 1971), et parce qu'il y davantage de pairs d'yeux qui peuvent détecter un danger qui s'approche (« *many eyes effect* », Pulliam 1973).

Outre la vigilance, les proies peuvent adopter d'autres ajustements comportementaux en réponse au risque de prédation, tel que l'utilisation d'habitats plus sûrs (Bergerud et al., 1983; Formanowicz et Bobka, 1988; Blumstein et Daniel, 2002; Ripple et Beschta, 2004), la réduction du temps passé à fourrager (Hughes et Ward, 1993; Abramsky et al., 2002), ou encore la restriction des déplacements (Sih et McCarthy, 2002). D'une manière générale, ces ajustements comportementaux au risque de prédation sont qualifiés d'effets indirects de la prédation, ou d'effets non-léthaux (*sensu* Lima et Dill, 1990). L'investissement dans ces ajustements se fait au détriment d'autres activités telles que la quête de nourriture (FitzGibbon et Lazarus, 1995; Frid et Dill, 2002 ; Blumstein et al., 2005), les soins parentaux, et les comportements reproducteurs (Gill et Sutherland, 2000). Il peut donc y avoir à moyen et long terme des coûts associés à ces ajustements comportementaux, i.e. survie et reproduction diminuées (Lima et Dill, 1990; Lima, 1998a). Ces coûts subis par les individus peuvent éventuellement se répercuter à des échelles supérieures: dynamique des populations altérées (Creel et al., 2007; Creel et Christianson, 2008) ou modification de la structure des communautés et du fonctionnement des écosystèmes (Brown et al., 1999; Ripple et Beschta, 2004).

La perturbation humaine peut être perçue comme un risque de prédation par les animaux, et peut donc les contraindre à ajuster leur comportement en conséquence (revues dans Frid et Dill, 2002; Stankowich et Blumstein, 2005). C'est probablement d'autant plus vrai pour la chasse, puisque dans ce cas les animaux risquent réellement de mourir, ce qui limite leur habituation au risque (mais voir Colman et al., 2001). Par exemple, chez les grands herbivores, le risque de chasse augmente les distances de fuite (revue dans Stankowich, 2008), modifie la sélection d'habitats (Swenson, 1982) et des sites d'alimentation (Benhaiem et al., 2008), et change les patrons d'activités (Kufeld et al., 1988).

Ces indicateurs comportementaux peuvent ainsi renseigner sur le niveau de perturbation subit par les animaux des populations exploitées. Toutefois, l'absence d'ajustement comportemental ne signifie pas forcément l'absence de perturbation (Gill et al., 2001). En effet, les animaux sont contraints d'acquérir des ressources pour survivre, et leur état physiologique influence leur comportement (McNamara et Houston, 1996). Les animaux en mauvaise condition physique, ou ceux qui ont davantage besoin de ressources, devraient ainsi mettre la priorité sur l'accès aux ressources au détriment de leur sécurité. Ils devraient donc être moins aptes à ajuster leur comportement, en dépit du risque encouru (Beale et Monaghan, 2004). Dans les systèmes où le risque de prédation est naturellement élevé, et où les proies compromettent déjà leur accès aux ressources pour réduire ce risque, on peut se demander si ces proies sont capables d'ajuster davantage leur comportement lorsque le risque de chasse est ajouté dans le système. C'est une question rarement abordée puisque la plupart des grand herbivores étudiés sont de l'hémisphère Nord, où le risque de prédation naturelle a considérablement été réduit par l'humain au cours des derniers siècles (Berger, 1999; Woodroffe, 2000). C'est néanmoins une question en devenir pour ces écosystèmes parce que les grands prédateurs, à l'instar du loup *Canis lupus* et de l'ours *Ursus arctos* en Europe, sont en train d'y effectuer leur retour.

CONTEXTE GÉOGRAPHIQUE DE LA THÈSE

Les savanes africaines

Il y a moins d'études portant sur les effets (directs et indirects) de la chasse aux trophées sur les grands herbivores d'Afrique par rapport à ceux d'Europe et d'Amérique du Nord. Or ceci n'est probablement pas en adéquation avec les préoccupations de conservation des populations de ces grands herbivores. En effet, les pratiques de gestion, mais aussi le déclin des grands carnivores avec l'expansion humaine (Berger, 1999; Woodroffe, 2000), ont favorisé l'augmentation des populations de grands herbivores dans l'hémisphère nord (e.g. en Europe: cerf élaphe, *Cervus elaphus*, Milner et al., 2006; chevreuil européen, *Capreolus capreolus*, Andersen et al., 1998; en Amérique du nord: cerf de Virginie, *Odocoileus virginianus*, Côté et al., 2004). Sur le plan de la conservation, la question de l'impact de la chasse aux trophées sur la dynamique de ces populations est donc généralement moins préoccupante pour ces populations que pour celles des grands herbivores africains.

La situation des grands herbivores d'Afrique est autrement plus préoccupante. D'abord parce que les savanes africaines abritent 105 espèces de grands herbivores, dont plus de 60 sont menacées, du fait notamment de la surchasse (IUCN, 2007). D'autre part, parce que la chasse aux trophées est particulièrement répandue en Afrique sub-saharienne, où elle est pratiquée dans 23 pays (Roulet, 2004). Elle génère 201 millions de dollars américains chaque année sur l'ensemble du continent, et couvre un territoire de ca. 1,400,000 km^2, soit 22% de plus que les parcs nationaux (revue dans Lindsey et al., 2007b). La chasse aux trophées est donc un acteur économique et un outil de conservation majeur sur ce continent (Bond, 1993). Toutefois, beaucoup d'états en Afrique manquent de moyens financiers et logistiques pour effectuer des suivis réguliers des populations animales. Les quotas de chasse ne sont donc pas toujours ajustés adéquatement, et de fait sont souvent excessifs (Elkan, 1994; Caro et al., 1998; Grobbelaar et Masulani, 2003).

Il y a en marge de ces considérations de gestion et de conservation d'autres intérêts à développer des études sur les conséquences de la chasse aux trophées en Afrique. Tout d'abord, la diversité de la guilde des grands herbivores africains donne la possibilité de mener des études comparatives entre plusieurs espèces d'herbivores. Ces études, encore rares, peuvent aider à mieux comprendre comment les caractéristiques spécifiques (e.g. régime alimentaire, pression de chasse) influencent les réponses comportementale, démographique et évolutive des grands herbivores à la chasse aux trophées. D'autre part, les savanes africaines abritent encore aujourd'hui une riche guilde de grands carnivores (Andersen et al., 2006). C'est là une opportunité unique d'étudier comment les grands herbivores ajustent leur comportement au double risque chasse / prédateurs naturels. C'est une question qui sera bientôt d'actualité en Europe et en Amérique du Nord avec le retour des populations de grands carnivores.

Chasse sportive au Zimbabwe

Au début des années 1960, les premières zones de chasse sportive (*Controlled Hunting Areas*) ont ouvert dans la vallée du Zambèze. Rapidement, la demande pour des camps de chasse a dépassé ce qui était proposé. En 1963, de nouvelles zones de chasse sportive ont donc été ouvertes à la frontière nord du Parc National de Hwange. Dans la même période s'est développée la chasse commerciale pour la production de viande (*game ranching*). Fin 1960, le gouvernement zimbabwéen se rend compte que ces systèmes de production basés sur la faune sauvage peuvent être très profitables, en particulier là où les sols peu ou pas fertiles ne sont pas propices aux systèmes de production traditionnels, i.e. élevage et agriculture (Fraser, 1970). Au début des années 1970, dans le nord-ouest du Zimbabwe, une grande zone d'élevage est achetée par le gouvernement, et est confiée au Département des Parcs Nationaux et de la Gestion de la Faune (*Department of National parks and Wild Life Management*, NPWLM) pour y développer le tourisme de chasse. Cette grande zone de ca. 8,000 km^2, le complexe de chasse de Matetsi (*Matetsi Safari Area*), fut alors divisée en sept concessions louées à des compagnies de chasse à partir de 1973. En 1975, la *Zimbabwe Parks and Wildlife Management Authority* (ZPWMA, anciennement NPWLM) donne à ces compagnies de chasse le droit d’utiliser et de gérer la faune sur leurs concessions. Ce fut le catalyseur du développement de la chasse touristique à travers le pays.

La chasse aux trophées est aujourd’hui pratiquée sur les aires de safaris d’état (*state safari areas*), les terres communales (*communal lands*), les forêts d’état (*indigenous forest areas*), et sur les terres privées (Heath et Machena, 1997). L’extension des zones de chasses aux terres privées et communales a permis au pays de doubler la superficie de ses aires protégées sans avoir eu à étendre ses réserves et parcs nationaux, dont la gestion est plus coûteuse pour l’état (Child, 1995). Le Zimbabwe est l’une des principales destinations de chasse touristique en Afrique (Lindsey et al., 2007b). La superficie allouée à la chasse représente 17% de la superficie du pays, avec 30,000km^2 sur des fermes commerciales privées, 14,000km^2, sur des fermes communales, 17,000km^2 sur des terres d’état, et 4,000km^2 sur des terres gérées par la Commission des Forêts (*Forestry Commission*). Cette activité génère 16 millions de dollars américains par an (Cumming, 1989; Cumming, 1999; Booth, 2002).

Les quotas de chasse dans les aires de safaris et les terres communales sont établis chaque année par la ZPWMA, sur la base de recensements aériens, de comptages routiers, et d’observations sur le terrain des *rangers* et des guides de chasse professionnels. Pour une aire donnée, les quotas alloués sont en théorie de l’ordre de 0.5% de la population pour l’éléphant, 2% pour la plupart des autres grands herbivores, et 8% pour les grands carnivores (Cumming, 1989). Là où ces quotas ont été respectés, les trophées récoltés sont semble-t-il restés de bonne qualité au fil des années, alors que là où ils ont été dépassés, la qualité des trophées a diminué (Booth et Jones, données non publiées dans Cumming, 1989). Dans le complexe de zones de chasse de Matetsi, les quotas sont considérés comme étant conservateurs, et sont soumis à des ajustements annuels en fonction de la qualité des trophées récoltés et de la taille estimée des populations (Cumming, 1989).

Zones d’étude

Cette thèse s’est déroulée dans l’écosystème de Hwange, composé du Parc National de Hwange et des zones environnantes (entre 17°45’S-20°30’S et 25°15’E-28°00’E), ca. 37,000 km^2, dans la province du Matabeleland au nord-ouest du Zimbabwe (Figure 1.1).

Cette zone est la principale composante zimbabwéenne de l’Aire de Conservation Transfrontalière de Kavango Zambezi (*Kavango Zambezi Transfrontier Conservation Area*), une mosaïque d’aires protégées et partiellement protégées, de corridors biologiques transfrontaliers partagés par l’Angola, le Botswana, la Namibie, la Zambie, et le Zimbabwe (Peace Parks Foundation, 2009).

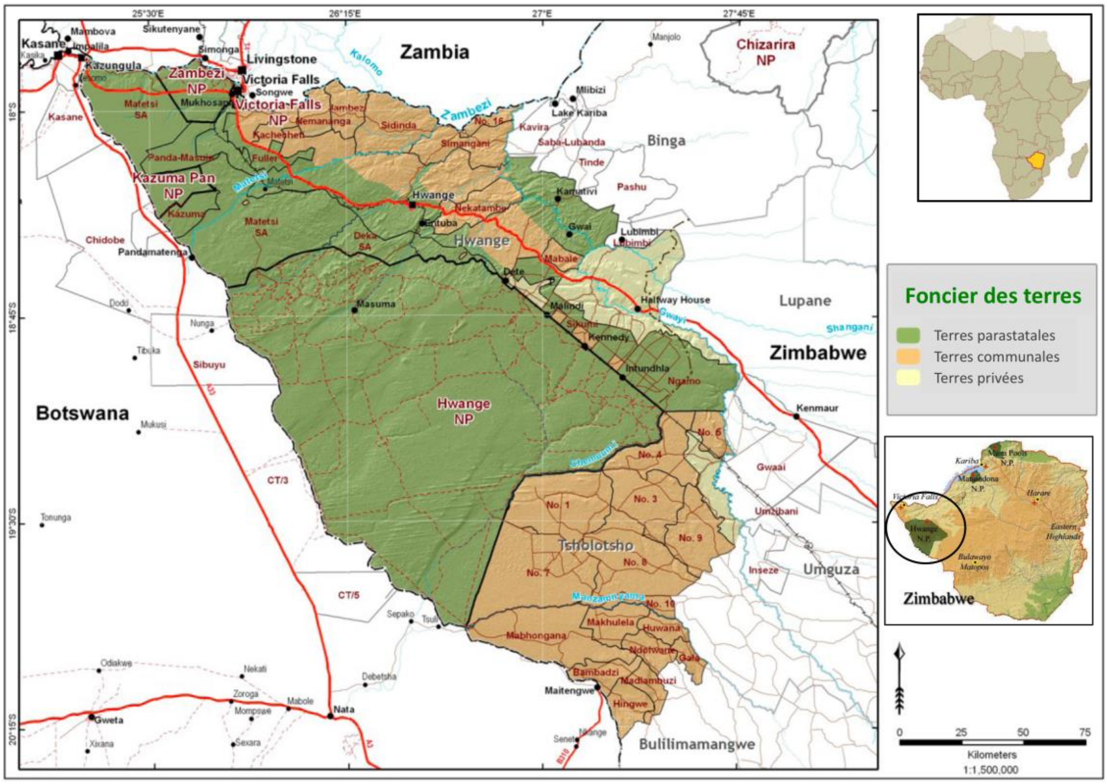

Figure 1.1: Foncier et type d’utilisation des terres dans l’écosystème de Hwange. NP : Parc National (*National Park*); SA : Aires de Safari (*Safari Areas*) (adaptée de Peace Parks Foundation, 2009).

L’écosystème de Hwange couvre divers types d’utilisation des terres, i.e. parcs nationaux, zones parastatales de chasse (*Safaris Areas*), zones privées de chasse (*Private Lands*), zones de foresterie (*Forest Lands*), terres communales (*Communal Lands*) (Figure 1.1). Le Parc National de Hwange (*Hwange National Park*, HNP), ca. 15,000 km^2, est une terre d’état administrée pas la ZPWMA. Les installations humaines sont interdites dans le parc national (à l’exception des principaux camps des officiers et employés: Main Camp, Sinamatella, et Robins), ainsi que l'utilisation des ressources (e.g. faune, bois, etc.). Des patrouilles d'anti braconnage y sont régulièrement conduites. Le complexe de chasse de Matetsi (*Matetsi Safari Area*, MSA), ca. 8,000 km^2, s'étend au nord-ouest de la frontière de HNP jusqu'à la Zambie (Figure 1.1). MSA est aussi une terre d'état administrée par la ZPWMA, mais louée aux compagnies de safaris depuis 1973 pour le tourisme cynégétique. Là aussi les installations humaines y sont interdites, mis à part le camp de Matetsi et les camps de chasse. Les compagnies ont de surcroît l'obligation de contrôler les activités illégales dans leurs concessions (e.g. braconnage), de gérer les feux de brousse, ainsi que l'approvisionnement en eau de surface. Les zones forestières de Sikumi et de Ngamo (*Forestry Areas*, FA), et la partie sud de l'Aire de Conservation Intensive de Gwaii (*Gwaii Intensive Conservation Area*, Gwaii), forment une zone tampon de ca. 3,100 km^2 le long de la frontière nord-est de HNP (Figure 1.1). Les FA sont des zones parastatales qui sont administrées par la Commission des Forêts, et qui autorisent en leur sein l'extraction de bois, le tourisme photographique et cynégétique. Les installations humaines n'y sont pas autorisées, mais des villages et terres communales se trouvent généralement dans leur périphérie immédiate, et sont source de braconnage, pâture illégale de cheptel domestique, exploitation illicite de bois à l'intérieur même des FA. Gwaii est un complexe de fermes privées où la chasse touristique est la principale activité économique depuis les années 1990. Le contrôle des activités humaines illégales est à la discrétion des propriétaires terriens, et tout comme pour les FA, la proximité de villages et de zones communales est source de braconnage et autres activités illégales. Enfin, les terres communales de Tsholotsho, ca. 8,000km^2, s'étendent à la frontière sud de HNP. C'est la zone limitrophe de HNP où l'impact du développement humain et de l'exploitation des ressources naturelles est le plus élevé (Peace Parks Foundation, 2009). La zone autorise la chasse touristique sous le programme CAMPFIRE[9] (Child, 1996), ainsi que l'exploitation forestière, des fermes de cultures et d'élevage et du pastoralisme.

Malgré les variations latitudinales de certaines variables environnementales, i.e. précipitations, températures, caractéristiques du sol, disponibilité en eau de surface (Peace Parks Foundation, 2009), l'ensemble de la zone d'étude est typique des savanes semi-

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[9] *Communal Areas Management Programme for Indigenous Resources*.

arides. L’écosystème Hwange reçoit en moyenne 650 mm de pluies par an, entre novembre et avril. La vegetation est typique des savanes australes dystrophique arborées et arbustives, avec quelques inclusions de prairies (Figure 1.2; Rogers, 1993; Ganzin et al., 2008). L’eau de surface est rare dans ces savanes et distribuée sporadiquement. On la trouve sous forme de rivières non permanentes et de dépressions qui retiennent l’eau de pluie pendant la saison des pluies (i.e. de novembre à mars) jusqu’au début de la saison sèche (i.e. d’avril à octobre). La plupart de ces sources d’eau sont en effet saisonnières, et s’assèchent assez rapidement au cours de la saison sèche. Durant cette dernière, l’eau n’est pratiquement plus présente qu’aux points d’eau artificiels, aménagés avec une pompe qui ramène à la surface l’eau souterraine. Ces points d’eau artificiels sont alors des zones d’intérêt en saison sèche, tant pour les espèces qui dépendent de l’eau de surface, que pour y effectuer des observations comportementales (Figure 1.3; Figure 1.4). La majorité des grands herbivores

Figure 1.2: Savane-type de l’écosystème Hwange (©Nicolas Ganzin).

de l'écosystème de Hwange sont en effet des espèces strictement dépendantes à l'eau de surface (Bothma et al., 2002). Avant la mise en place des points d'eau artificiels à partir de 1935, les espèces animales qui peuplaient cet écosystème étaient principalement des espèces de milieu xérique, comme le gemsbok (*Oryx gazella beisa*). Depuis, la mise en place de ces points a favorisé l'expansion démographique et géographique des herbivores dépendants à l'eau, à l'instar par exemple de l'éléphant (Davidson, 1967) et de l'impala (Bourgarel, 2004).

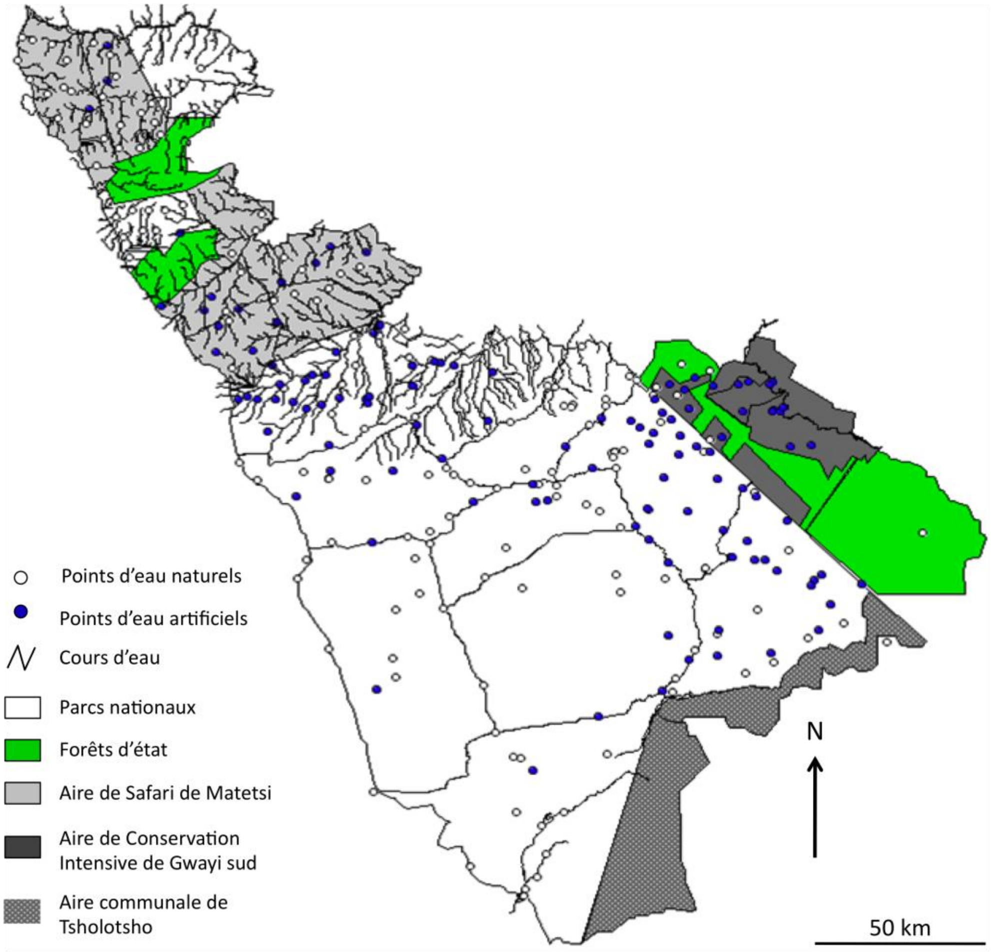

Figure 1.3: Distribution spatiale des points d'eau naturels et artificiels, ainsi que des principaux cours d'eau dans les zones d'étude.

Figure 1.4: Zone de point d'eau typique de l'écosystème Hwange (©Marion Valeix).

<u>Espèces à l'étude</u>

Nous avons choisi de mettre l'emphase sur l'impala (*Aepyceros melampus*), le grand koudou (*Tragelaphus strepsiceros*), et l'hippotrague noir (*Hippotragus niger*) comme principaux modèles biologiques dans cette thèse (Figure 1.5).

Figure 1.5: Mâles adultes d'impala, hippotrague noir et grand koudou (de gauche à droite) (©Maël Le Corre).

Ce sont trois espèces de ruminants grégaires relativement communes dans les zones d’études, dépendantes à l’eau, et donc facilement observables autour des points d’eau. Mais ces trois espèces diffèrent de par leur vulnérabilité aux prédateurs naturels, leur contrainte à l’eau de surface, et leur valeur auprès des chasseurs de trophées. Le grand koudou, et l’impala dans une moindre mesure, sont davantage vulnérables aux prédateurs naturel (i.e. lion *Panthera leo*, hyène *Crocuta crocuta*, léopard *Panthera pardus*, lycaon *Lycaon pictus*, et guépard *Acinonyx jubatus*) que l’hippotrague noir (Hayward et Kerley, 2005; Hayward, 2006; Hayward et al., 2006a, b, c; Drouet-Hoguet, 2007; Loveridge et al., 2007a; Rasmussen, 2009). Les brouteurs, comme le grand koudou, dépendent moins de l’eau de surface que les paisseurs comme l’hippotrague noir, et les herbivores au régime alimentaire mixte comme l’impala (Western, 1975). D’autre part, à mesure que la saison sèche avance, et que les zones de pâtures deviennent plus rares, les paisseurs doivent chercher des zones d’alimentation de plus en plus éloignées des points d’eau (Redfern et al., 2003; Rahimi et Owen-Smith, 2007). Ceci peut augmenter leurs dépenses d’énergie et le risque de prédation. Par conséquent, l’hippotrague noir devrait être davantage contrainte par l’accès à l’eau de surface que le grand koudou, et l’impala. Les trois espèces sont populaires auprès des chasseurs de trophées (Lindsey et al., 2006). Chasser l’hippotrague noir coûte néanmoins plus cher que chasser le grand koudou, ou l’impala, i.e. environ 23,000, 6,500, et 5,500 Dollars américains respectivement (Booth, 2009; Zindele Safaris, 2012). Les clients chasseurs devraient donc se montrer plus sélectifs dans leur quête de trophées lorsqu’ils chassent l’hippotrague noir par rapport au grand koudou, et surtout à l’impala.

Ces différences de vulnérabilité aux prédateurs naturels, de contrainte à l’eau de surface, et de valeur des trophées, permettent de faire des études comparatives originales. On s’attend ainsi par exemple à ce que l’amplitude des ajustements comportementaux en réponse au risque de chasse change entre les trois espèces, ainsi que les changements temporels de longueurs de cornes.

OBJECTIFS ET PLAN DE LA THÈSE

Des préoccupations de gestion aux questions de recherche

Le tourisme de faune au Zimbabwe, photographique et cynégétique, s'est considérablement développé au cours des années 1960 à 1990. Ce succès commercial a encouragé une utilisation des terres orientée vers la faune, et a donc largement favorisé l'augmentation des populations animales au cours de cette période, en particulier sur les terres privées et communales. Depuis 2000 et la réforme agraire, beaucoup de terres privées jusqu'à lors tournées vers le tourisme de faune, ont été morcelées, redistribuées et transformées en terres d'agriculture de subsistance et d'élevage. S'en est suivi un déclin des populations animales sur ces terres (Bond et Cumming, 2006). Durant la même période, la ZPWMA a dû faire face à une chute drastique du tourisme de faune, photographique en particulier, et à une inflation galopante. Deux facteurs qui ont considérablement réduit les moyens logistiques de la ZPWMA, et donc son investissement dans la gestion de la faune, en particulier dans le suivi des populations animales à l'extérieur des parcs nationaux.

Le projet de recherche *Hwange Environmental Research for Development* (HERD) dirigé par Hervé Fritz[10], dans lequel s'inscrit cette thèse, est né de la collaboration entre la ZPWMA, le CNRS[11], le CIRAD[12], l'Ambassade de France au Zimbabwe, ainsi que deux universités zimbabwéennes (NUST[13] et TREP-UZ[14]). Ce projet a une mission double. Une mission de conservation qui vise à fournir un appui scientifique et logistique pour la conservation d'espèces rares de la région de Hwange. Une mission académique, qui traduit en questions de recherche scientifique les problématiques de gestion des aires protégées, pour comprendre le fonctionnement des populations de grands herbivores et leur impact sur leur écosystème, et éventuellement proposer des scénarios de gestion.

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[10] Directeur de recherche UMR CNRS 5558 – Laboratoire de Biométrie et Biologie Evolutive.

[11] Centre National de Recherche Scientifique.

[12] Centre International de Recherche en Agronomie pour le Développement.

[13] *National University of Science and Technology*.

[14] *Tropical Resources Ecology Programme of the University of Zimbabwe*.

Objectifs :

Cette thèse s’inscrit donc dans cette démarche avec un **objectif double**. Il s’agit d’une part sur le plan scientifique de **1)** voir si, et comment, la chasse aux trophées affecte indirectement (**Partie I**), et directement (**Partie II**) les populations exploitées de grands herbivores africains. Dans le cadre de l’étude des effets indirects, la principale hypothèse est que la chasse perturbe le comportement des animaux. Sous cette hypothèse, les animaux des populations chassées devraient ajuster leur comportement de façon à réduire le risque de chasse, et ce au détriment du comportement d’approvisionnement. Concernant les effets directs, deux principales hypothèses peuvent être formulées. Tout d’abord, le prélèvement sélectif exercé par la chasse aux trophées peut créer une sélection artificielle en faveur des individus aux cornes plus petites. Sous cette hypothèse, la taille des cornes des individus récoltés devrait en moyenne diminuer au fil des années. Ensuite, puisque les grandes cornes sont essentiellement arborées par les mâles adultes, la chasse aux trophées devrait altérer la structure des populations chassées. Sous cette hypothèse, ces dernières devraient présenter des proportions de mâles adultes plus faibles que celles des populations non chassées.

D’autre part, il s’agit **2)** de faire un ‘état des lieux’ post-réforme agraire des populations de grands herbivores dans les zones de chasse, et en particulier des tendances temporelles de leurs densités et de la taille des cornes sur les animaux récoltés par les chasseurs de trophées.

Plan de thèse

La **Partie I** de la thèse s’articule donc autour des effets indirects de la chasse aux trophées. Nous cherchons à établir s’il y a des ajustements comportementaux des grands herbivores africains en réponse au risque de chasse, et si oui, comment ces ajustements contrarient l’approvisionnement en eau de surface, ressource limitante des savanes semi-arides. Nous comparons en particulier le patron temporel d’accès aux points d’eau (***Chapitre 2***) des groups d’ongulés, et les niveaux de vigilance de leurs individus (***Chapitre 3***) entre le Parc National de Hwange et les zones de chasse périphériques.

Dans la **Partie II,** nous étudions les effets directs de la chasse aux trophées en observant les tendances temporelles de la taille des cornes des mâles récoltés, la modification de la structure des populations exploitées (i.e. proportions de mâles adultes et taille de groupes), et les densités de populations. Le ***Chapitre 4*** fait le point sur les tendances temporelles et spatiales de la taille des trophées (i.e. longueur des cornes des mâles) au cours des 30 dernières années dans les zones de chasse de Matetsi. Nous cherchons en particulier à déterminer si la pression sélective de la chasse aux trophées a conduit à une diminution de la longueur des cornes au fil des ans. Nous comparons ces tendances pour l'impala, le grand koudou et l'hippotrague noir, qui sont soumis à des pressions sélectives de chasse aux trophées différentes. Dans le ***Chapitre 5*** nous comparons la structure des populations de plusieurs espèces de grands herbivores, en particulier les proportions de mâles adultes, la taille des groupes, ainsi que les densités entre les zones de chasse de Matetsi et le Parc National de Hwange. Le ***Chapitre 6*** illustre le rôle de conservation que peuvent tenir les zones de chasse en abritant des densités d'espèces rares parfois plus élevées que dans les parcs nationaux, avec l'exemple de l'hippotrague noir.

La figure 1.6 représente de façon schématique les principaux mécanismes, indirects et directs, par lesquels la chasse aux trophées peut influencer la dynamique des grands herbivores africains.

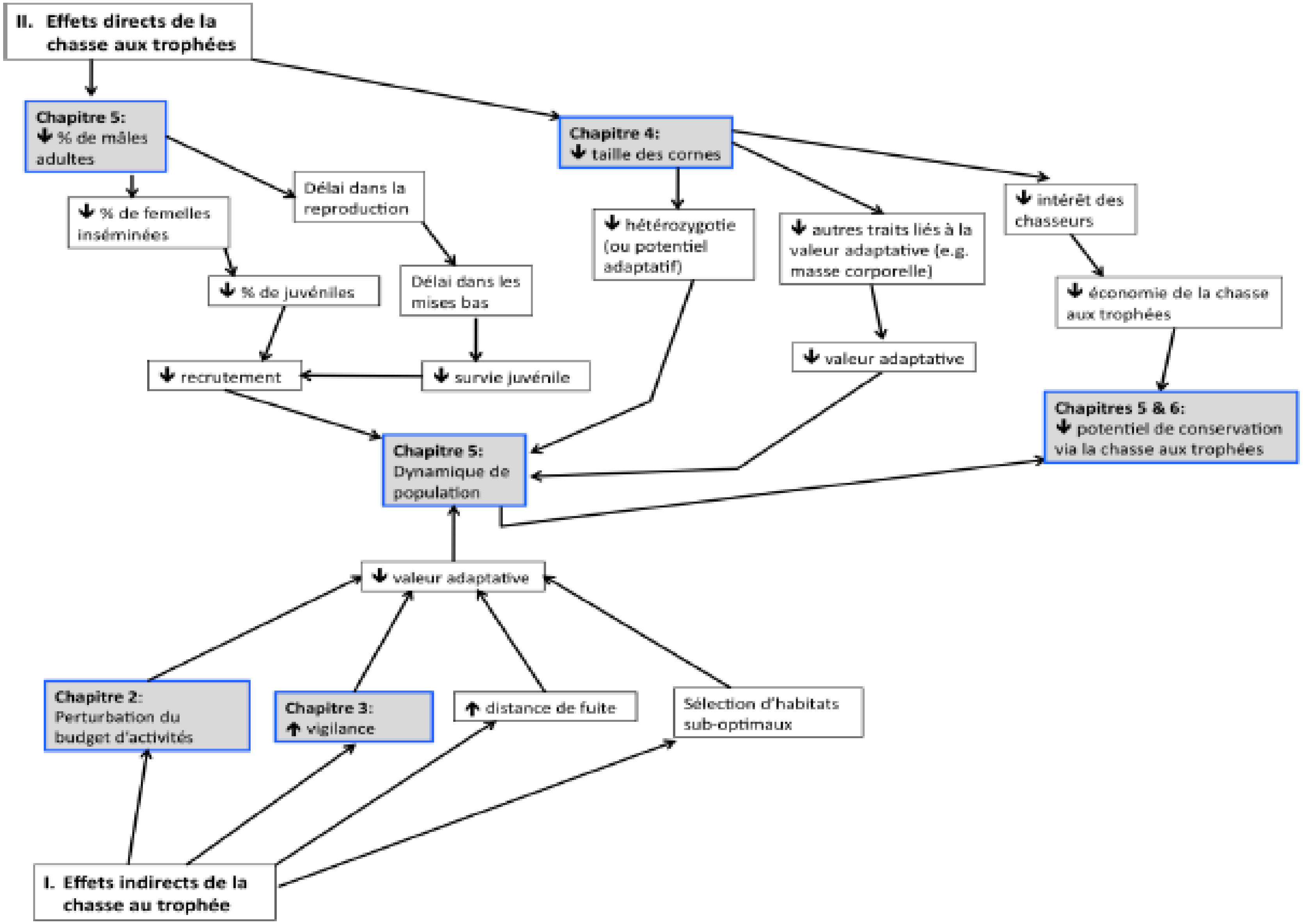

Figure 1.6: Schéma conceptuel des effets indirects et directs de la chasse aux trophées sur la dynamique des populations exploitées de grands herbivores, et le potentiel de conservation des zones de chasse aux trophées. Les cadres ombragés sont les chapitres abordés dans cette thèse.

Partie I

Effets indirects de la chasse aux trophées: les ajustements comportementaux en réponse au risque de chasse

CHAPITRE 2
AUX POINTS D’EAU DE NUIT EN ZONES DE CHASSE

African ungulates and their drinking problems: hunting and predation risks constrain access to water

WILLIAM-GEORGES CROSMARY, MARION VALEIX, HERVÉ FRITZ, HILLARY MADZIKANDA AND STEEVE D. CÔTÉ

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Résumé

Les proies ajustent leur comportement afin de minimiser le risque de prédation exercé par leurs prédateurs naturels. Lorsque chassées, elles peuvent avoir à ajuster davantage, ou différemment, leur comportement pour faire face à ce risque additionnel de mortalité. Nous avons examiné si les ongulés africains ajustaient leur comportement en réponse au risque de chasse, i.e. risque d'être abattu par les chasseurs. Nous nous attendions à ce que ces ongulés viennent aux points d'eau, ressource clef dans les savanes africaines, davantage de nuit dans les zones de chasse pour réduire le risque d'être chassé. Dans le Parc National de Hwange, Zimbabwe, et les zones de chasse avoisinantes, nous avons suivi plusieurs points d'eau pour noter les heures de boisson des groupes d'impala (*Aepyceros melampus*), de grand koudou (*Tragelaphus strepsiceros*), et d'hippotrague noir (*Hippotragus niger*). Dans le Parc National de Hwange, les trois espèces ont évité de venir aux points d'eau de nuit, période au risque de prédation naturelle élevé. Dans les zones de chasse, les trois espèces sont venues aux points d'eau plus souvent la nuit que dans le parc national. Néanmoins, les impalas et les grands koudous étaient moins enclins à venir aux points d'eau de nuit que les hippotragues noirs, même si le risque de chasse était équivalent pour les trois espèces. Nos résultats suggèrent que la chasse peut contraindre les ongulés africains à basculer leurs visites aux points d'eau à la nuit. Mais l'amplitude de cette bascule s'avère être limitée par le risque de prédation exercé par les grands carnivores, principalement actifs la nuit. Nous concluons que les proies ajustent leur comportement en réponse au risque additionnel exercé par la chasse.

Abstract

Prey make several behavioural adjustments to minimize the risk of predation by their natural predators. When hunted, however, they may have to adjust their behaviour further or differently to cope with this additional mortality risk. Here, we investigated whether African large ungulates would adjust their behaviour in response to hunting risk, i.e. risk of being shot by human hunters. We predicted that they would shift their use of surface water, a key and scarce resource in African savannas, from day hours to night hours to reduce the risk of encountering human hunters. In Hwange National Park, Zimbabwe, we monitored waterholes to record the temporal drinking niche of three non-hunted ungulates, i.e. impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and sable antelope (*Hippotragus niger*). We also monitored waterholes in hunting areas in the vicinity of Hwange National Park. In Hwange National Park, the three species avoided waterholes at night, when the risk of natural predation was higher. Conversely in the hunting areas, all species visited waterholes more often at night than in Hwange National Park. Impala and greater kudu, however, were less prone to switch towards night-time use of waterholes in hunting areas compared to sable antelope, while the three species were exposed to similar hunting risk. Our results suggest that hunting may force African ungulates to shift their visits at waterholes from day hours towards night hours, but that the magnitude of this shift may be constrained by the predation risk imposed by large nocturnal carnivores. We conclude that species preyed upon by natural predators adjust their anti-predator behaviour in response to the additional risk of predation imposed by hunting.

Keywords: ecology of fear; behavioural adjustments; predation risk; hunting risk; ungulates; waterholes.

Introduction

With ongoing increase of human disturbance on wildlife habitats, there is growing concern about how disturbance stimuli may affect animal behaviour (Geist, 1970; Caro, 1999a). Animals respond to human disturbance similarly to predation risk, i.e. by adjusting their behaviour in order to reduce the disturbance, for example by increasing flight initiation distance or vigilance, or by shifting habitats (reviewed in Stankowich et Blumstein, 2005). There may be medium to long-term costs associated with behavioural adjustments, e.g. lower resource intake rate, lower diet quality, or decreased mating opportunities (Lima et Dill, 1990; Lima, 1998a). The repercussions of these non-lethal effects of predation or disturbance (sensu Lima, 1998a) might therefore alter the fitness of individuals, affect population dynamics (Creel et al., 2007; Creel et Christianson, 2008), and ultimately community structure and ecosystem functioning (Brown et al., 1999; Ripple et Beschta, 2004).

Hunting may be considered an extreme type of human disturbance as individuals from harvested populations experience a direct risk of mortality. Hunting disturbance disrupts normal activities, alters diurnal activity rhythms, and increases flight initiation distances in many waterbird species (reviewed in Madsen et Fox, 1995). In large ungulates, studies have reported increased flight initiation distance in response to hunting disturbance (reviewed in Stankowich, 2008). However, much less is known about long-term behavioural responses such as shifts in habitat use (Swenson, 1982) and feeding sites (Benhaiem et al., 2008), or changes in activity patterns (Kufeld et al., 1988).

Here we address an example of long-term behavioural adjustment to hunting in large game ungulates. We assessed whether ungulates adjust their temporal use of key and scarce resources in response to hunting risk, i.e. risk of being shot by human hunters. A common behavioural response of prey to predation risk is to avoid risky areas where predators are abundant (Ripple et Beschta, 2004; Creel et al., 2005; Valeix et al., 2009a). In certain circumstances, however, spatial avoidance of predators may not be possible, particularly when prey have no choice but to use risky areas to access rare and scattered resources where predators might look for them. Under such situations, prey may shift their niche along the time axis to reduce temporal overlap with predator activity (reviewed in

Kronfeld-Schor et Dayan, 2003). While such temporal adjustments have been illustrated in some predator-prey studies (Kotler et al., 1991; Fenn et Macdonald, 1995; Roth et Lima, 2007; Valeix et al., 2009b), much less has been reported on hunted species (but see Kilgo et al., 1998; Sunde et al. 2009), particularly on how hunting risk may affect resource utilization.

Semi-arid African savannas are excellent ecosystems to investigate how hunting risk may constrain temporal access of ungulates to scarce water resources. First, hunting is very common in Africa, more particularly sport hunting (Lindsey et al., 2007b), i.e. recreational hunting practised by paying tourists. Yet, only few studies have reported behavioural adjustments in response to hunting risk in African ungulates (Matson et al., 2005; Setsaas et al., 2007; Caro, 1999b) compared to ungulates from the Northern hemisphere, e.g. reindeer (*Rangifer tarandus*) (reviewed in Reimers et Colman, 2006). Second, surface-water is limited in African semi-arid savannas. Hence, even though the risk of encountering predators (Valeix et al., 2009a, b) and human hunters (e.g. Harrison et Bates, 1991 for ungulates in deserts of the Middle East) may be high, most ungulates have to come to waterholes almost daily to satisfy their drinking requirements. Third, the richness of African ungulate communities provides the opportunity for original comparative studies. While behavioural changes in harvested populations may be used as indicators of species sensitivity to human hunting, Gill et al. (2001) stressed that behavioural indicators might not always adequately reflect animal response to human disturbance. For instance, animals of lower condition, or that undergo higher constraints on resource requirements, are less likely to adjust their behaviour in response to human disturbance (e.g. Beale et Monaghan, 2004). Likewise, behavioural response to hunting risk may expose ungulate species to their natural predator (e.g. Kilgo et al., 1998). Species therefore more vulnerable to natural predators might be less likely to adjust their behaviour to human hunting risk. Multi-species studies are rare and greatly needed to understand how specific ecological constraints may influence behavioural responses to human hunting.

We investigated how different African ungulate species, impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and sable antelope (*Hippotragus niger*), adjust their temporal use of waterholes in response to hunting risk. We hypothesized that ungulates would shift their temporal use of waterholes to night-time in hunting areas to decrease temporal overlap with human hunters, in comparison to protected areas where ungulates drink mainly during daytime (Valeix et al., 2007a). We expected this shift to be partial, notably because of the constraint exerted by predation risk at night, as the main predators in our study area are mostly nocturnal, i.e. lion (*Panthera leo*) (Schaller, 1972), spotted hyaena (*Crocuta crocuta*) (Kruuk, 1972). Further, we predicted the magnitude of the shift to vary according to species vulnerability to natural predation. The species more often preyed upon, i.e. greater kudu, should perform a shift of lower magnitude than others.

Methods

Study site

Hwange National Park (nonHA) in northwestern Zimbabwe (19°00'S, 26°30'E) is ca. 15 000 km^2. Sport hunting is allowed and practised in governmental safari areas and private concessions around nonHA: Matetsi Safari Area South (MSA South, 1 890 km^2) and Gwaii Intensive Conservation Area South (Gwaii ICA South, ca. 880 km^2) (Fig. 2.1).The hunting mode practised in these hunting areas is sport hunting, and thus harvest usually represents a small fraction of total population size, contrary to culling or uncontrolled poaching. Harvest rates are traditionally set at ca. 2% of population size for most ungulates in Zimbabwean hunting areas (Cumming, 1989). During the study period, we estimated per-capita hunting risk based on the ratio of hunting quotas over population size estimates for the three species. We found, as Cumming (1989), that percentages of harvested individuals were ca. 2% of population size, i.e. 2.5%, 1.7%, and 1.4% for impala, greater kudu, and sable antelope, respectively. This implies similar per capita risk of human predation for all ungulate species. These Hunting Areas (HA) act as buffers between the National Park and human settlements where subsistence agriculture is the principal activity and wildlife is only present at low densities (Dunham 2002).

Vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of grasslands, dominated mainly by *Colophospermum mopane*, *Combretum spp.*, *Acacia spp.*, *Baikiaea plurijuga* and *Terminalia sericea* (Rogers, 1993). The rainy season ranges from November to April, and long-term annual rainfall averages 613 mm

(Chamaillé-Jammes et al., 2006). Surface water is mainly found in natural and artificially filled waterholes, and in some rare rivers. During the dry season, natural waterholes and rivers dry up and most of the surface water available to animals is found in artificially filled waterholes and river pools.

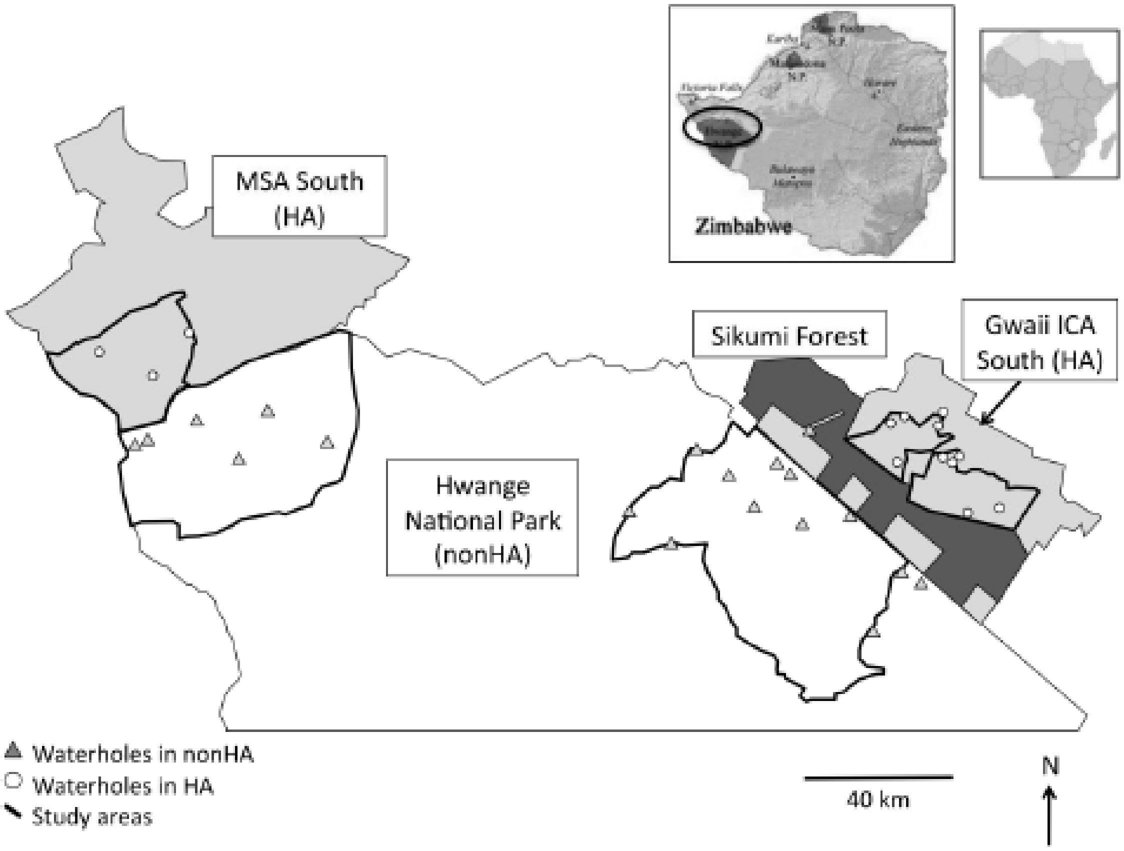

Figure 2.1: Hwange National Park (nonHA) and adjacent hunting areas (Gwaii ICA South and MSA south, HA) in Zimbabwe. Study area is delineated by thick black lines.

No sport hunting occurs in nonHA, but the Zimbabwe Parks and Wildlife Management Authority (ZPWMA) allocates quotas to its staff for food rations, mainly on elephants (*Loxodonta africana*), and buffalos (*Syncerus caffer*), while other ungulates have not been allocated since 2007. In the surrounding HA, hunting season ranges from March to December since the mid 1970s. Ungulates are strictly hunted during daytime, from dawn (around 6am) to dusk (around 7pm). Hunters are not allowed to hunt from vehicles and hunts are performed on foot. Overall, the abundance of large carnivores appears to be comparable between the study HAs and their adjacent nonHA areas (Elliot, 2007; Table 2.1). Hence the main difference between HA and nonHA is the predation risk due to hunting by humans. We thus disposed of a contrasted system, where the risk undergone by ungulates in nonHA was exclusively exerted by natural predators, whereas the risk in HA originated both from natural predators and human hunters (further information on the different study areas is provided in Table 2.1).

Our study area covered, in the peripheral HA, the hunting concessions from which we had obtained the authorisation to carry out wildlife surveys during the study period, i.e. Unit 3 in MSA South (ca. 360 km^2), and four hunting properties in Gwaii ICA South (ca. 300 km^2) (Fig. 2.1). In nonHA, we chose to cover the blocks that were adjacent to those hunting concessions, i.e. Main camp (ca. 1 300 km^2), and Robins (ca. 1 000 km^2) in the northern part of Hwange National Park (Fig. 2.1). Therefore, the hunting concessions and their adjacent blocks in nonHA presented similar vegetation types and environmental conditions (i.e. rainfall, temperature, soil characteristics) (Ganzin et al., 2008; Peace Parks Foundation, 2009).

Observations

We monitored waterholes in nonHA and surrounding HA in 2007 and 2008, during the hot dry season (from August to October). In HA, we selected waterholes on the basis of availability of standing water, and signs of recent ungulates presence, i.e. fresh spoors and faeces. We monitored only once nine waterholes in 2007, and seven waterholes in 2008. Only two waterholes were surveyed both years (i.e. thirteen different waterholes in total). In nonHA, each waterhole is surveyed once a year since the 1970s by Wildlife and Environment Zimbabwe (WEZ) and ZPWMA. Accounting for vegetation similarities with HA as well as water availability, we randomly selected nineteen waterholes from the existing database in 2007, and thirteen in 2008 (i.e. nineteen different waterholes in total).

Monitoring consisted in 24-h counts during full moon periods to document temporal drinking niches of ungulates at waterholes. Full moon nights guaranty good visibility conditions to carry out observations, particularly in the areas surrounding waterholes which are characterized by the absence of vegetation. Observations were conducted with

Table 2.1: Superficies, density of waterholes, total length of roads, density of impala, greater kudu, and sable antelope, abundance of the main large carnivores (Elliot, 2007), in Main Camp (hunting-free area, nonHA), Gwaii ICA South (hunting area, HA), Robins (hunting-free area, nonHA), and Unit 3 of MSA South (hunting area, HA), Zimbabwe.

	Main Camp *(nonHA)*	Gwaii ICA South *(HA)*	Robins *(nonHA)*	Unit 3/ MSA South *(HA)*
Area (km^2)	1300	300	1000	360
Waterhole densities (nb/100km^2)	1.23	4.34	1.3	2.5
Roads length (km)	325	172	400	263
Impala density (indiv./km^2)	1.43 (CV=0.47)	NA	5.45 (CV=0.31)	3.0 (CV=0.15)
Greater kudu density (indiv./km^2)	1.59 (CV=0.24)	NA	1.52 (CV=0.36)	2.5 (CV=0.20)
Sable antelope density (indiv./km^2)	0.22 (CV=0.44)	NA	NA	1.0 (CV=0.45)
Lion density estimated by spoor transects (indiv./100km^2)	2.6	2.2	*	4.5
Lion density estimated by call-up surveys (indiv./100km^2)	2.8-5.5	2-3.9	*	5.3-7.7
Hyaena density estimated by call-up surveys (indiv./100km^2)	11.3-22.1	5.5-10.9	*	6.5-11.7
Hyaena spoor densities (spoors/100km^2)	27.2	11.6	*	26.5
Leopard spoor densities (spoors/100km^2)	1.2	4.2	NA	1.3
Wild dog spoor densities (spoors/100km^2)	0.4	1.6	NA	0.2
Cheetah spoor densities (spoors/100km^2)	0.1	0.5	NA	1.5

CV is the coefficient of variation associated to density estimates calculated by Distance Sampling (Buckland et al., 2001).

* indicates that density estimates are not available but are comparable to Main Camp (Loveridge et Elliot, Personal Communication).

For call-up surveys, the lower density estimate corresponds to the 2.5km response range, and the higher to the 3.2km response range (Elliot, 2007).

NAs indicate the absence of estimate.

binoculars or spotting scopes (15–45 x) from platforms, tree hides, or from a car parked at a distance of ca. 100m from waterholes to avoid disturbing animals. We recorded time at which groups arrived at waterholes, as well as species, group size, and presence/absence of young. We accounted for group size and presence of young as co-factors in the decision to access waterholes during daytime or at night, as both group size ("many eyes effect" – Pulliam, 1973; and "dilution effect" – Hamilton, 1971; Dehn, 1990) and presence of young (Berger, 1991; Burger et Gochfeld, 1994) are known to influence antipredator behaviours.

Study species

We focused on two browsers: impala and greater kudu, and one woodland grazer: sable antelope. These ungulates are strictly dependent on surface water, and visit waterholes on a regular basis mostly during daytime in nonHA (Valeix et al., 2007a). In the study area, the main predators are lions and spotted hyaenas (Table 2.1). Lions are ambush predators and many lion kills (~40%) occur close to a waterhole (Valeix et al., 2009a, 2011). Hyaenas are cursorial predators that have been reported to commonly hunt in waterhole areas (Salnicki et al., 2001; Personal Observations). Both carnivore species are nocturnal and their visits to waterholes occur mainly at night (70% and 80% of the lion visits recorded during the monitoring occurred at night in nonHA and HA respectively, and 90% and 100% of the hyaena visits occurred at night in nonHA and HA respectively) (see also Appendix 2.1). Lions were not hunted in HAs at the time of the study because of a moratorium on lion hunting that took place in the study area between 2005 and 2008, and hyaenas are very rarely targeted by hunters.

Whereas impalas were more abundant than greater kudus and sable antelopes in the study area (ca. 8 800 impalas, 4 700 greater kudus, and 1 200 sable antelopes), they represented less than 5% of lions' diet (Loveridge et al., 2007a). The four-fold difference observed between the abundance of greater kudu and the abundance of sable antelope was respected in the diet of lions, with greater kudu representing up to 24%, and sable antelope less than 5% (Loveridge et al., 2007a). This is consistent with other African systems where lions prey upon greater kudu and sable antelope in accordance with the abundance of these prey species, whereas impala is avoided (reviewed in Hayward et Kerley, 2005). However, in the nearby Kruger National Park, South Africa, 61.3% of encounters between impala and lion led to hunts (Funston et al., 2001). Therefore, despite impala not being a preferred prey species for lion, impalas probably do not consider lions as a low level threat. Hyaenas do not prefer any prey species (Hayward, 2006). Impala and greater kudu, which are among the commonest prey species consumed by hyaenas, are taken in proportion to their relative abundance. Sable antelope, however, is more likely to be avoided. In our study area, greater kudu, impala, and sable antelope respectively represented 8-12%, 5-10%, and less than 5% of hyaenas' diet (Drouet-Hoguet, 2007). However, ca. 80% of hyaena's food was acquired by scavenging (Drouet-Hoguet, 2007), whereas ca. 16% was obtained by hunt. Impala represented 56% of the prey species hunted, greater kudu 19%, whereas sable antelope was not hunted (Drouet-Hoguet, 2007). For the secondary large carnivore species of the study area, i.e. leopard (*Panthera pardus*), wild dog (*Lycaon pictus*), and cheetah (*Acinonyx jubatus*), there is no equivalent information on diet composition. Nonetheless, reviews on these large carnivore diets (Hayward et al., 2006a, b, c) indicate that leopards preferentially prey upon impala, consume greater kudu in proportion of its relative abundance, and tend to avoid sable antelope. Wild dogs preferentially prey upon greater kudu and impala (see Rasmussen, 2009 for our study area), whereas consume sable antelope in proportion of their relative abundance. Cheetahs preferentially prey upon impala, consume greater kudu in accordance to their relative abundance, and tend to avoid sable antelope. Overall, these diet studies suggest that greater kudu, and impala to a lower extent, are more vulnerable to their natural predators than sable antelope.

The magnitude of behavioural adjustments in hunted populations is likely to increase with hunting pressure (Caro, 1999b; Matson et al., 2005). During road counts carried out in HA in the late dry season 2007 and 2008, we encountered 4 groups of impala/100km, 3 groups of greater kudu/100km, and 1.4 groups of sable antelope/100km. In the meantime, the realized hunting quotas, i.e. actual numbers of animals shot, were 1.2 times higher for impala than for greater kudu, and 4 times higher for impala than for sable antelope (ZPWMA Unpublished data). Therefore, considering the dilution effect, the human hunting risk perceived by groups of ungulates was comparable among the three species. Thus, the three species differed mainly by their exposure to natural predators, and we therefore expected impala and greater kudu to be less prone to shift their visits at waterholes during night-time than sable antelopes when hunted because of their higher exposure to natural predators then. We observed 226 groups of impala (131 in nonHA, 95 in HA), 188 groups of greater kudu (149 in nonHA, 39 in HA) and 63 groups of sable antelope (41 in nonHA, 22 in HA).

Statistical analyses

Drinking temporal niche at waterholes was approximated by the arrival time of groups at waterholes. We plotted a frequency distribution of group observations at waterholes by hour using Oriana 2.0 software for circular data (Fisher, 1993). We used the group as the statistical unit. Mean arrival times per species were compared with the Watson-Williams test for circular means (Fisher, 1993). To test whether waterholes were more frequently visited at night in HA than in nonHA, we compared the respective temporal distributions of visits at waterholes between the two zones. To determine the expected number of visits in HA during daytime (from 6am to 7pm) and at night (from 7pm to 6am), we used the distribution of visits at waterholes in nonHA where there was no sport hunting. We then compared the expected distribution with the observed distribution in HA using a contingency table (following Zar, 1984), with the Pearson's chi-squared test with Yates' continuity correction, and the Fisher's exact test for frequencies that were smaller than five.

For each species, we investigated the effects of zone (nonHA or HA), group size, and presence/absence of young on the probability of arriving at a waterhole at night with a logistic regression model. The respective effects of group size and presence of young, however, may be confounded for the three species because the two factors were correlated (Wilcoxon signed-rank test with continuity correction: impala, $V = 20301$, $r = 0.10$, $N = 201$, $P < 0.001$, $N = 201$; greater kudu, $V = 17020$, $r = 0.19$, $N = 184$, $P < 0.001$; sable antelope, $V = 1770$, $r = 0.64$, $N = 59$, $P < 0.001$), the large groups including young. We included all possible interactions between fixed effects but none was statistically significant. To compare the probabilities of visiting waterholes at night between species, we used a logistic regression with species and zone as factors, and their interaction. For all logistic models, we used the Akaike information criterion (AIC) to select the best model (Burnham et Anderson, 2002). The model with the lowest AIC value (i.e. the best compromise between accuracy and precision) was retained. When ΔAIC between two models was < 2, we selected the simplest model according to the parsimony rules (Burnham et Anderson, 2002). All statistical analyses were generalized linear mixed models, with year and waterhole fitted as random effects, using R *lme4* package (http://cran.r-project.org/web/packages/lme4/index.html).

Results

Groups of all three species visited waterholes preferentially during daytime, generally avoiding night hours (Fig. 2.2). However, avoidance of waterholes during night-time was less marked in HA, where proportionally more groups came at night compared to nonHA. In nonHA, 6% of groups of impala, less than 1% of groups of greater kudu, 10% of groups of sable antelope visited waterholes at night. Conversely in HA, 24% of groups of impala, 20% of groups of greater kudu, and 50% of groups of sable antelope visited waterholes at night. These differences between day and night were significant for the three species (impala, Pearson's chi-squared test: $X^2_1 = 13.76$, $N = 226$, $P < 0.001$; greater kudu, Fisher test: $N = 188$, $P < 0.001$; sable antelope, Fisher test: $N = 63$, $P = 0.001$) (Fig. 2.3).

Average arrival times at waterholes did not differ between nonHA and HA for impala (Watson-Williams test: $F_{1,\ 221} = 1.56$, $P = 0.2$; Fig. 2.2), and greater kudu (Watson-Williams test: $F_{1,\ 185} = 0.15$, $P = 0.7$; Fig. 2.2). Sable antelope arrived at waterholes later in HA than in nonHA (Watson-Williams test: $F_{1,\ 59} = 18{,}68$, $P < 0.0001$; average arrival time in nonHA = 11:40; average arrival time in HA = 18:56). Circular variances associated with average arrival times were higher in HA than in nonHA (impala: circular standard deviation in nonHA = 65°, HA = 90°; greater kudu: nonHA = 41°, HA = 86°; sable antelope: nonHA = 56°, HA = 89°). The distribution of arrival times was thus more scattered in HA than in nonHA. Temporal distributions of arrival times were more concentrated during daytime in nonHA than in HA, particularly during the hottest hours of the day (between 10am and 4pm): for impala, 49.6% of groups were observed during the hottest hours of the day in nonHA, as opposed to 35.9% in HA; for greater kudu, it was 68.5% in nonHA vs 31.5% in HA; and for sable antelope, 51% in nonHA vs 30% in HA.

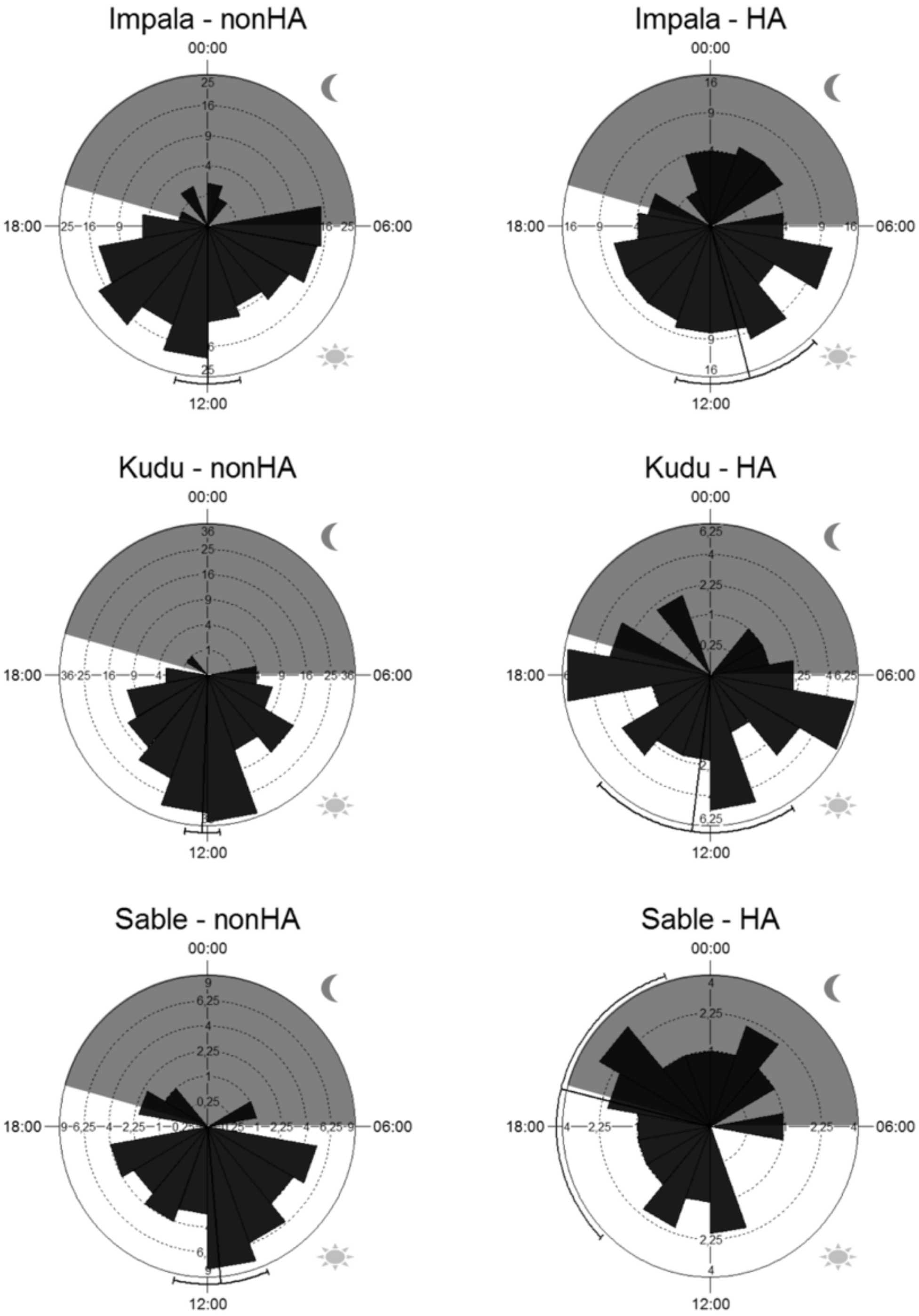

Figure 2.2: Temporal visits at waterholes by groups of impala, greater kudu, and sable antelope in 2007 and 2008 during daytime (6am to 7pm) and night time (7pm to 6am) under two contrasted situations: natural predation and no sport hunting (nonHA, Hwange National Park, Zimbabwe) vs natural predation and sport hunting (HA). Each bar length represents the number of groups that came during each hour and the area of each bar is thus proportional to the frequency of group visits. The black line underneath each graph indicates mean arrival time, with 95% confidence interval.

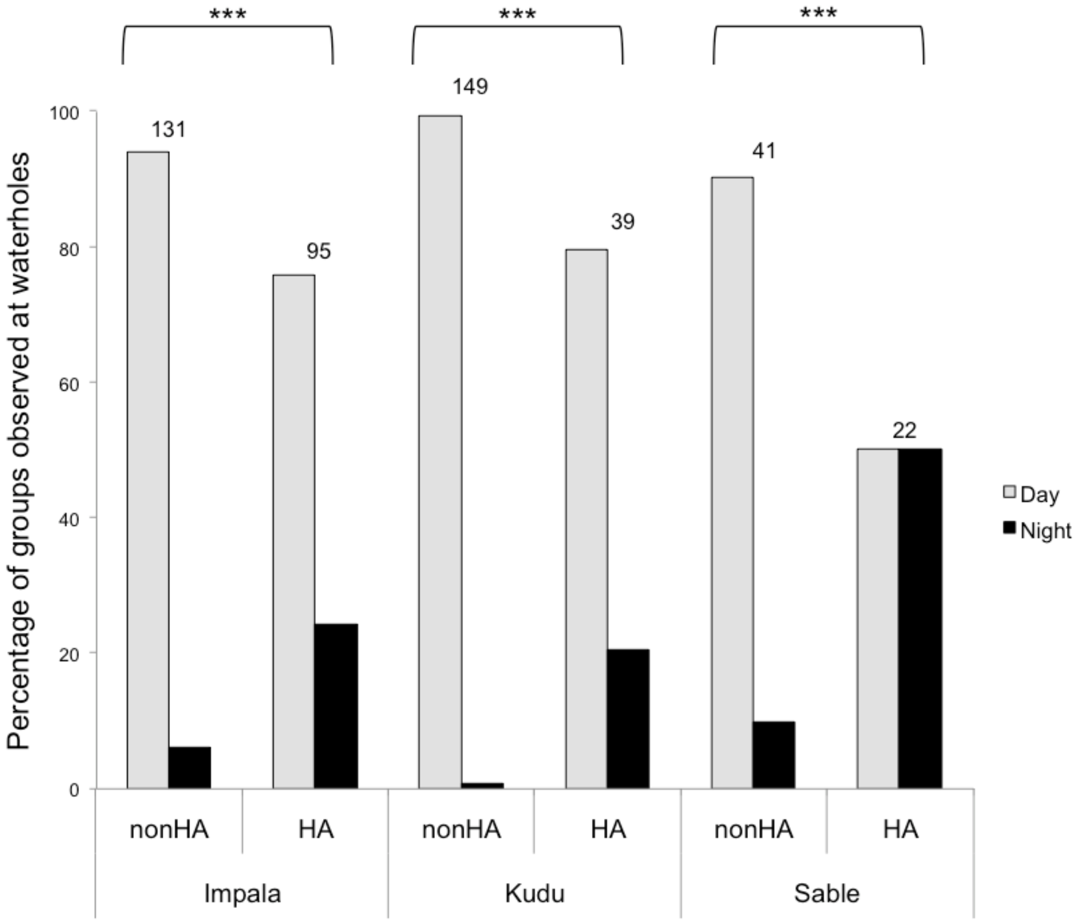

Figure 2.3: Effect of sport hunting on the attendance at waterholes of groups of impala, greater kudu, and sable antelope during daytime (6am to 7pm) vs night time (7pm to 6am) in 2007-08. Zones with natural predation and no sport hunting (nonHA, Hwange National Park, Zimbabwe) vs natural predation and sport hunting (HA) are compared. Figures above the bars indicate the number of groups present at waterholes in each zone. Statistical tests are from comparisons of frequencies within contingency tables, but results are presented as percentages for clarity. *** p<0.001.

Logistic regressions confirmed that the probability of visiting waterholes at night was higher in HA than in nonHA for the three species (Table 2.2; impala: estimate ± SE = 2.3 ± 1.0; greater kudu: estimate ± SE = 3.7 ± 1.1; sable antelope: estimate ± SE = 7.0 ± 2.2). Moreover, the probability to visit waterholes at night was lower for groups with young in impala (Table 2.2; estimate ± SE = –2.6 ± 1.2), but not for greater kudu (Table 2.2). For sable antelope, whereas the presence of young was retained in the selected model (Table

Table 2.2: Summary of the logistic-regression modelling the probability of visiting waterholes at night as a function of the zone (Hunting Area, HA vs Non Hunting Area, nonHA), group size and status (i.e. presence/absence of young) for groups of impala, greater kudu, and sable antelope in Hwange National Park (Zimbabwe) and the surrounding hunting areas in 2007 and 2008.

models	K[a]	AIC	ΔAIC
impala			
null	22	127.1	7.8
zone	24	125.2	5.9
status	24	121.6	2.3
group size	24	128.7	9.4
zone + status	**25**	**119.3**	**0.0**
zone + group size	25	127.0	7.7
group size + status	25	123.3	4.0
zone + group size + status	26	120.5	1.2
kudu			
null	22	55.4	5.4
zone	**24**	**51.0**	**1**
status	24	56.5	6.5
group size	24	55.6	5.6
zone + status	25	50.0	0
zone + group size	25	50.8	0.8
group size + status	25	57.5	7.5
zone + group size + status	26	51.6	1.6
sable			
null	15	58.0	21
zone	16	49.7	12.7
status	16	48.1	11.1
group size	16	55.2	18.2
zone + status	**17**	**37.0**	**0**
zone + group size	17	42.7	5.7
group size + status	17	50.6	13.6
zone + group size + status	18	38.9	1.9

[a] Number of parameters. It includes the random factor “waterholes”.

2.2), its effect on the probability to visit waterholes at night was highly variable (estimate ± SE = −20.4 ± 2322.1). Group size was not retained in the selected models, and therefore did not affect the probability of visiting waterholes at night for any of the three species (Table 2.2).

Sable antelope had a higher probability of visiting waterholes at night compared to impala and greater kudu in HA, but not in nonHA (Fig. 2.4). In HA, impala and kudu had a similar probability of visiting waterholes during night-time, whereas in nonHA greater kudu had a lower chance of visiting waterholes at night than the two other species.

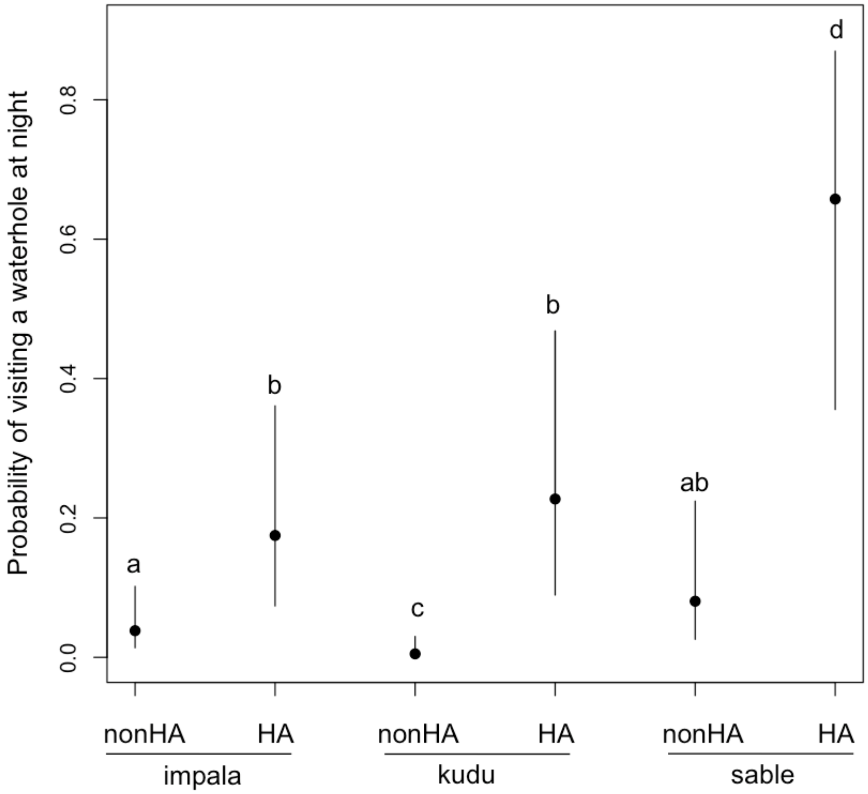

Figure 2.4: Probabilities of visiting waterholes at night (7pm to 6am) for impala, greater kudu, and sable antelope in 2007 and 2008. Zones with natural predation and no sport hunting (nonHA, Hwange National Park, Zimbabwe) vs natural predation and sport hunting (HA) are compared. Estimates from logistic regression models and their confidence intervals (back-transformed) are shown. Estimates with different letters are different at $p<0.05$ (e.g. a situation with letter “a” is significantly different from a situation with a letter “b” or “c” or “d”, but not from a situation with “ab”).

Discussion

Prey may shift their niche along the time axis to reduce temporal overlap with predator activity (reviewed in Kronfeld-Schor et Dayan, 2003; Caro, 2005). Human hunters, similarly to natural predators, may also induce a temporal adjustment of the niche in hunted populations (e.g. Kilgo et al., 1998). Here, we used African ungulates in semi-arid savannas and their use of waterholes to show how prey adjust their temporal niche in response to both the risk of natural predation by large carnivores mostly at night, and the risk of being hunted by human hunters during the day. Groups of impala, greater kudu, and sable antelope visited waterholes more often at night in hunting areas than in non-hunting areas (Hwange National Park), where visits at waterholes were almost exclusively diurnal. The temporal pattern of access to water was concentrated around the hottest hours of the day in the protected area, particularly for greater kudu, while it was scattered throughout the day in hunting areas. More interestingly, we observed that groups of impala and greater kudu were less prone to switch their access to water towards night-time in hunting areas compared to groups of sable antelope, although they were exposed to similar hunting risk.

The diurnal use of waterholes by ungulates in African savannas is largely dictated by the circadian rhythms and physiology of these ungulates (Finch, 1972; Ayeni, 1977; Valeix et al., 2007b). It may also be a tactic to decrease the risk of encountering the main natural predators of these ecosystems (Valeix et al., 2009a), which visit waterholes essentially at night to drink or to hunt their prey. Whereas the activity of ungulates at waterholes was almost exclusively diurnal in the protected area (see also Weir et Davison, 1965; Valeix et al., 2007a for Hwange National Park; and Ayeni, 1975 for Tsavo National Park, Kenya), a large proportion of the groups (24% for impala, 20% for greater kudu, and 50% for sable antelope) visited waterholes at night in hunting areas. We hypothesize that this significant temporal shift towards nocturnal use of waterholes in hunting areas is a behavioural adjustment of ungulates to the risk of being hunted by humans during daytime. The increase of nocturnal activities (e.g. movements, foraging, social interactions) as a way to escape human disturbance occurring during daytime has been largely documented in birds, e.g. Riddington et al., 1996 for brent goose (*Branta b. bernicla*), Burger et Gochfeld, 1991 for sanderling (*Calidris alba*), but less so in ungulates (but see Kilgo et al., 1998 for white-tailed deer (*Odocoileus virginianus*); Sunde et al., 2009 for red deer (*Cervus elaphus*)).

The significant temporal shift towards nocturnal use of waterholes exposes ungulates to their natural predators. Hence, ungulates in the hunting areas face a trade-off between the risk of natural predation and the risk of being hunted. Such trade-off is poorly understood because most studies on hunting are carried out on ungulates of temperate ecosystems (Altmann, 1958 for moose (*Alces alces*) and elk (*Cervus canadensis*); de Boer et al., 2004; Benhaiem et al., 2008 for roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*); reviewed in Reimers et Colman, 2006 for caribou and reindeer) where the diversity and densities of predators have been largely reduced by human (Berger, 1999; Andersen et al., 2006). In comparison, African savannas still host a rich guild of large carnivores. Our results showed greater circular variances associated with mean arrival time at waterholes for the three species in hunting areas, whereas the great majority of observations were made during the hottest hours of the day (from 10am to 4pm) in the protected area. In African savannas, the hottest hours of the day coincide with the period when large carnivores are less active (Kruuk, 1972; Schaller, 1972). Consequently, ungulates drinking at waterholes during this period may benefit from a reduced risk of natural predation. Conversely, visits of ungulates at waterholes were more randomly distributed over the day in hunting areas. As a consequence, their whereabouts were less predictable to human hunters. Random anti-predator behaviour of prey may also be an efficient tactic against predators; for instance, Scannell et al. (2010) recently demonstrated that prey that scan at random are more difficult to catch by predators. The decrease in the predictability of the temporal pattern of visits at waterholes may be an alternative tactic adopted by ungulates to partly reduce hunting risk during daytime without completely shifting towards night-time, and thus limiting increased exposure to natural predators.

The magnitude of the temporal shift in the use of waterholes was expected to vary according to species vulnerability to natural predation and exposure to hunting. Because the three species differed mainly by their exposure to natural predation, we predicted that greater kudu, and to a lesser extent impala, should be less prone to shift their visits at waterholes during night-time than sable antelope. Interestingly, sable antelope showed the greatest shift to night use of waterholes in hunting areas whereas greater kudu and impala showed the smallest shift. Such results are consistent with the observation that greater kudu is the second most frequent prey of lions (after buffalo) (Loveridge et al., 2007a), and that greater kudu and impala represent a greater share than sable antelope of hyaena diet in Hwange National Park (Drouet-Hoguet, 2007), while sable antelope has never been identified as a main prey for one of the large carnivores in Hwange National Park. Previous studies in this ecosystem have shown that greater kudu was particularly responsive to the immediate risk of predation by lions (Valeix et al., 2009b; Périquet et al., 2010). Hence, it is not surprising that greater kudu and impala shifted less their temporal niche at waterholes towards the night in hunting areas, and sable antelope, which appears less sensitive to natural predation, shifted the most to night use of waterholes in hunting areas. Our results indicate that the higher the risk of natural predation, the lower the probability to shift to night use of waterholes to avoid human hunters.

It is worth mentioning that we limit our conclusions to nights during which visibility is good, since we carried out our observations during full moon nights. Lower visibility condition during other nights may change prey perception of natural predation risk. Ayeni (1975) observed that many herbivores in Tsavo National Park, Kenya, drank later into the night on moonlit nights than on moonless nights, probably because it is then much more difficult to detect approaching predators. Under moonless or cloudy nights, the situation of ungulates would be therefore even more complicated than during full moon nights because natural predation risk is probably enhanced because of lower visibility.

The propensity to shift to nocturnal use of waterholes was also influenced by presence of young in impala, and in sable antelope to a lower extent, the probability to come to waterholes at night being higher for groups with young than for groups without young. Because young are highly vulnerable to predators, groups with young normally adjust their behaviour to compensate for increased vulnerability (see Burger et Gochfeld, 1994 for increased vigilance; Hamel et Côté, 2007 for avoidance of risky areas and risky hours). In greater kudu however, the presence of young in groups had no significant influence. Since greater kudu is the most vulnerable prey species, it may not be less dangerous for groups without young to come at night at waterholes than for groups with young. This however remains to be investigated. We found no effect of group size on the probability to come to waterholes at night. Perceived predation risk, however, was expected to be lower in larger groups because of the greater number of individuals to scan the surroundings to detect approaching predators (“many-eyes effect”, Pulliam, 1973) and a dilution effect (Hamilton, 1971; Dehn, 1990). At night, because of the lower light conditions (even under full moon light), a greater number of individuals may not sufficiently offset the increased risk of predation due to the presence of young in large groups. Moreover, the risk for groups with young to be targeted by natural predators might be higher than the risk to be targeted by human hunters, the latter usually seeking trophy males, often solitary or found in small bachelor groups.

We cannot fully exclude other potential alternative explanations to the nocturnal shift observed in hunting areas, e.g. differences in environmental conditions, tourism, and natural predation. The studied hunting areas and Hwange National Park were adjacent and showed similar soil composition, vegetation structure, temperature and rainfall characteristics (Ganzin et al., 2008; Peace Parks Foundation, 2009). Moreover, the diurnal preferential use of waterholes by African ungulates has been shown in other ecosystems, e.g. Tsavo National Park in Kenya (Ayeni, 1975), Etosha National Park in Namibia (Preez et Grobler, 1977). Therefore, differences in environmental conditions are unlikely to be responsible for the difference in the temporal pattern of visits at waterholes observed in our study between Hwange National Park and the adjacent peripheral hunting areas. Tourism was generally low in Zimbabwe during our study (2007-2008) due to the economic and political crisis, and there were very few tourists in Hwange National Park and the peripheral hunting areas. Finally, densities of natural predators, proportion of waterholes visited by these natural predators, and the temporal pattern of these visits were similar between Hwange National Park and the peripheral hunting areas (Table 2.1, Appendix 2.1). Hence, we interpreted that the shift made to night use of waterholes in hunting areas was a response to the risk of being hunted by human hunters during the day, which is the main difference between the national park and the peripheral hunting areas.

Our study illustrates how sport hunting influence the ecology of ungulates in a system where ungulates have to face a trade-off between the risk of natural predation by carnivores and the risk of being hunted, the former being higher at night and the latter during the day. To our knowledge, this is one of the first attempts to explore such trade-off, and one of the rare studies that contrasts different species. The three study species were characterized by a gradient in the risk of natural predation leading to a gradient in the shift made to night use of waterholes in hunting areas. The species more often preyed upon, i.e. greater kudu, performed the shift of the lowest magnitude, whereas the species less preyed upon, i.e. sable antelope, performed the shift of the highest magnitude. Because our study did not measure the potential costs associated with the shift of visits to waterholes towards night-time in hunting areas, we cannot assume that this behavioural response to hunting risk has any impact on individual fitness. In order to better understand the role that sport hunting and induced behavioural adjustments can play in ungulate population dynamics, there is a need to investigate whether these differences of behaviour between hunting-free areas and hunting areas actually lead to measurable costs in terms of physiology and survival, e.g. greater exposure to natural predators, alteration of thermoregulation, or changes in time budget.

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CHAPITRE 3
DE LA VIGILANCE, MAIS PAS TROP

Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk

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Sous presse dans «Animal Behaviour».

Résumé

L’amplitude des ajustements comportementaux des proies en réponse au risque de prédation est limitée par la nécessité de maintenir l’acquisition des ressources. Dans les systèmes au risque de prédation élevé, les proies sont contraintes d’ajuster leur comportement, souvent au détriment de l’acquisition des ressources. Dans un tel cas, les proies pourraient être à la limite des ajustements possibles, et donc être incapables d’ajuster davantage leur comportement lorsque le risque de chasse augmente. Nous avons examiné si les grands herbivores africains ajustaient leur comportement en réponse au risque de chasse. Dans le Parc National de Hwange (HNP) et les zones de chasse voisines (HA), Zimbabwe, nous avons suivi le comportement aux points d’eau de l’impala (*Aepyceros melampus*), du grand koudou (*Tragelaphus strepsiceros*), et de l’hippotrague noir (*Hippotragus niger*). Une fois les groupes entrés dans les zones de point d’eau, leur probabilité de retourner dans la végétation sans avoir bu était supérieure en HA que dans HNP. Les individus étaient plus vigilants en HA que dans HNP en approchant et en quittant les points d’eau, mais pas pendant la période d’abreuvement. Ceci suggère que l’abreuvement était priorisé sur la vigilance lorsque les individus avaient atteint les points d’eau. Le temps passé par les groupes dans les zones de point d’eau n’était pas plus long en HA que dans HNP, bien que les individus étaient plus vigilants. Ceci suggère que les groupes limitaient leur exposition aux chasseurs. Les grands koudous étaient les plus vigilants, probablement parce que les plus vulnérables aux prédateurs naturels. Les hippotragues noirs étaient les moins enclins à compromettre leur acquisition d’eau de surface. Par conséquence, les deux espèces ont montré des ajustements comportementaux en réponse au risque de chasse d’amplitude moindre que l’impala. Notre étude multi spécifique illustre comment la vulnérabilité aux prédateurs naturels et les contraintes environnementales interagissent pour limiter les réponses comportementales des grands herbivores au risque de chasse.

Abstract

The magnitude of behavioural adjustments by prey in response to predation risk is constrained by the necessity to maintain resource acquisition. In systems with high predation risk, prey display adjustments that can challenge resource acquisition. In such case, they may be at a limit and could not adjust further their behaviour when hunting risk is increased (i.e. risk caused by human hunters). We investigated whether large African herbivores may adjust their behaviour in response to hunting risk. In Hwange National Park (HNP) and the peripheral hunting areas (HA), Zimbabwe, we monitored behaviour of impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and sable antelope (*Hippotragus niger*) at waterhole areas. Once groups had entered waterhole areas, the probability they returned into vegetation cover without drinking was higher in HA than in HNP. Individuals were more vigilant in HA than in HNP when they were approaching and leaving waterholes, but not during drinking. This suggests that drinking was prioritized over vigilance once individuals had reached waterholes. The time groups spent in waterhole areas was not longer in HA compared to HNP, though individuals were more vigilant, suggesting that groups limited their exposure time to hunters. Greater kudus were the most vigilant probably because they are the most vulnerable to predators. Sable antelopes were the least prone to compromise the acquisition of surface water. Both species consequently displayed adjustments of lower magnitude than impala in response to hunting risk. Our multi-species study illustrates how vulnerability to natural predators and environmental constraints interplay to limit the behavioural responses of large herbivores to hunting risk.

Keywords: vigilance, behavioural adjustments, predation risk, hunting risk, large African herbivores, waterholes.

Introduction

Human activities are potential sources of disturbance in animal populations (reviewed in Frid et Dill, 2002). This is particularly true for hunting because animals experience direct risk of mortality, and therefore habituation is unlikely in hunted populations (but see Colman et al., 2001). Hunting, like predation, may directly alter population dynamics by increasing mortality (e.g. Caughley, 1977; Solberg et al., 1999), and indirectly by constraining animals to divert part of their time and energy budgets to safety-related behaviours (e.g. waterbird species reviewed in Madsen et Fox, 1995; large herbivores in Kufeld et al., 1988; Benhaiem et al., 2008). Investment into antipredator behaviours may compromise other fitness-enhancing activities (e.g. foraging), potentially altering individuals reproductive output or/and long-term survival (Lima et Dill, 1990; Lima, 1998), and eventually population dynamics (Creel et Christianson, 2008).

Sutherland (1998) stressed the importance of behavioural studies in conservation biology, but Gill et al. (2001) argued that behavioural indicators may not always properly indicate animal responses to human disturbance. Animals may indeed make state-dependent decisions (McNamara et Houston, 1996). Those in lower condition, or that have higher constraints on resource requirements, may be less likely than others to adjust their behaviour in response to human disturbance (e.g. Beale et Monaghan, 2004). The trade-off between safety and exposure to predators should be particularly exacerbated in systems with high predation risk and environmental constraints on resource acquisition. In such systems, further behavioural adjustments in response to any extra risk, such as hunting, may be highly constrained by the need to satisfy resource requirements.

Understanding constraints acting on behavioural adjustments is of prime importance for the conservation and management of hunted populations. This is particularly true for ungulates because they are hunted worldwide (Festa-Bianchet, 2007), and play a determinant role in ecosystems functioning (Gordon et al., 2004). Whether and how much ungulates under high predation risk can adjust their behaviour to hunting risk remains, however, poorly understood. Most studies have focused on ungulates of temperate ecosystems (e.g. moose, *Alces alces*: Altmann, 1958; white-tailed deer, *Odocoileus virginianus*: Kilgo et al., 1998; caribou, *Rangifer tarandus*: Aastrup, 2000; roe deer, *Capreolus capreolus*: de Boer et al., 2004), where human activities have widely reduced the diversity and densities of natural predators (Berger, 1999). These studies were moreover essentially on single species, which limits our understanding of how different ecological requirements may influence behavioural response to disturbance (Blumstein et al., 2005).

Here, we investigated behavioural adjustments displayed by ungulates of semi-arid African savannas in response to hunting risk. African savannas host the richest guild of large terrestrial carnivores (Andersen et al., 2006), and ungulates in this system must thus adjust their behaviour in response to predation risk (e.g. FitzGibbon, 1994; Hunter et Skinner, 1998). Semi-arid African savannas are moreover characterised by the scarcity of surface-water. Water is a key resource for African ungulates that are compelled to regularly come at waterholes to drink, despite the high risk of being ambushed by predators (Valeix et al., 2009, 2010). This problem is accentuated during the dry season as surface water becomes scarcer. McNamara et Houston (1996) suggested that as physiological stress increases, resource acquisition is prioritized at the expense of investment into antipredator behaviours. At the peak of the dry season, drinking should thus be prioritized over investments into antipredator behaviours (e.g. Valeix et al., 2007; Périquet et al., 2010). The capacity of African ungulates to further adjust the balance between antipredator behaviours and water acquisition during the dry season in response to extra risk induced by hunting should thus be limited.

We compared antipredator behaviours and water acquisition of impala *Aepyceros melampus*, greater kudu *Tragelaphus strepsiceros*, and sable antelope *Hippotragus niger*, at waterholes in a hunting-free environment, Hwange National Park, Zimbabwe, and in the neighbouring hunting areas. We expected these ungulates to leave waterholes without drinking more often (i.e. lower drinking probability), and to be more vigilant, in hunting areas than in the National Park. We, however, predicted the magnitude of these behavioural adjustments to vary with species, according to vulnerability to natural predation and the constraint of surface water availability. Greater kudu, as the species most often preyed upon (Drouet-Hoguet, 2007; Loveridge et al., 2007), should display the strongest antipredator behavioural adjustments in the National Park, i.e. lowest drinking probability and highest vigilance at waterholes. In order to maintain water acquisition, greater kudu should be less likely to adjust further these behaviours in hunting areas in spite of increased overall predation risk, i.e. drinking probability should decrease less and vigilance should increase less than for species less vulnerable to predation. Sable antelope, that are particularly constrained by access to surface-water (Western, 1975; Redfern et al., 2003; Rahimi et Owen-Smith, 2007), should be less likely to compromise drinking opportunities once at waterholes compared to impala and greater kudu. We expect sable antelope to display the highest drinking probability and the lowest vigilance level in the National Park, and to minimally adjust these behaviours in hunting areas despite the hunting risk. Impala, being less vulnerable to natural predation than greater kudu, and less constrained by access to surface water than sable antelope, should be able to decrease their drinking probability and to increase their vigilance in response to hunting risk more than the two other species.

Methods

Study site

We conducted field observations during the late dry season (from August to late-October) in 2008, in Hwange National Park (hereafter HNP), ca. 15 000 km^2, north western Zimbabwe (19°00’S, 26°30’E), and in some immediately adjacent Hunting Areas (hereafter HA), i.e. Matetsi Safari Area South (hereafter MSA South), ca. 1 890 km^2, and Gwaii Intensive Conservation Area South (hereafter Gwaii ICA South), ca. 880 km^2. In the peripheral HA, we selected hunting concessions from which we had obtained the authorisation to carry out wildlife surveys during the study period, i.e. Unit 3 in MSA South (ca. 360 km^2), and four hunting properties in Gwaii ICA South (ca. 300 km^2) (Fig. 3.1). In nonHA, we covered the blocks that were adjacent to those hunting concessions, i.e. Main camp (ca. 1 300 km^2), and Robins (ca. 1 000 km^2) in the northern part of Hwange National Park (Fig. 3.1). The hunting concessions and their adjacent blocks in nonHA selected for our study presented similar vegetation types and environmental conditions (i.e. rainfall, temperature, soil characteristics) (Ganzin et al., 2008; Peace Parks Foundation, 2009).

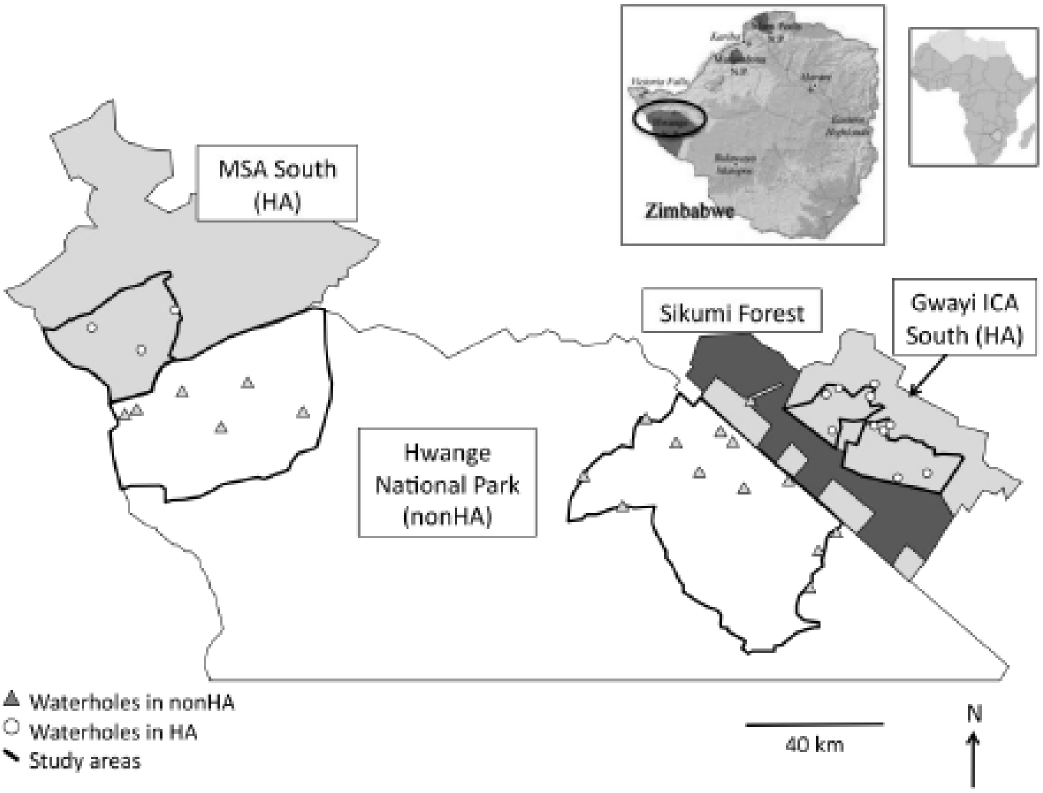


Figure 3.1: Hwange National Park (HNP, hunting-free area) and adjacent sport hunting areas (HA, Gwaii ICA South and MSA south) in Zimbabwe, Africa. The study area is delineated by thick black lines. Triangles represent locations of waterholes monitored within HNP, and circles locations of waterholes monitored in HA.

The study area received an average of 600 mm of rainfall during the rainy season for the past century, 830 mm in 2008, with most of it falling from December to March. Most water sources are seasonal, and eventually dry up after the early part of the dry season (i.e. June/July). Provision of water during the dry season mainly relies on artificially filled waterholes through ground water pumping in both HNP and HA (Fig. 3.1). Vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of grasslands (Rogers, 1993), with dominance of *Colophospermum mopane* and *Combretum spp.* in MSA South and Robins, and dominance of *Baikiaea plurijuga, Burkea Africana, Terminalia sericea,* and *Brachystegia* woodlands in Main Camp and Gwaii ICA South (Ganzin et al., 2008).

HNP is a state land administrated by Zimbabwe Parks and Wildlife Management Authority (ZPWMA). No permanent settlement is allowed within the limits of HNP, aside from ZPWMA headquarters and some outlying ranger posts. Illegal activities, such as poaching and timber extraction, are controlled and limited by regular vehicle and foot patrols both in HNP and in HA, hence we could assume the level of illegal exploitation was similar between the two land uses. Trophy hunting does not occur in HNP, but ZPWMA allocates quotas to its staff for food rations, mainly on elephants (*Loxodonta africana*), and buffalos (*Syncerus caffer*). Trophy hunting occurs since the 1970s in HA, and hunting season ranges from March to December. Hunters are theoretically not allowed to hunt at waterholes (ZPWMA personal communication), but occasionally do in practise, and often visit waterhole areas to look for signs of targeted species. Overall, the main large predators of the system were present in HNP and HA in comparable densities (Elliot, 2007; Crosmary et al., 2012). We thus studied a contrasted system, where the risk undergone by ungulates in nonHA was exclusively exerted by natural predators, whereas the risk in HA originated both from natural predators and human hunters (Crosmary et al., 2012).

Study species

We selected impala, greater kudu, and sable antelope as our biological models because they shared common ecological features (ruminants, group living), were fairly observable in reasonable numbers (see densities in Crosmary et al., 2012), were harvested in the hunting areas, but contrasted in their vulnerability to natural predators and dependency to surface-water. Greater kudu, and impala to a lesser extent, are preyed upon by every large African carnivore species, and are among the main prey species in these predator diets (reviewed in Hayward, 2006; Hayward et Kerley, 2005; Hayward et al., 2006a, b, c). Sable antelope conversely is essentially preyed upon by lion (*Panthera leo*) (Hayward et Kerley, 2005), and generally avoided by other large carnivores. Diet studies in our system confirmed this broad African pattern (Loveridge et al., 2007; Drouet-Hoguet, 2007; Rasmussen, 2009). Greater kudu, and impala to a lesser extent, were therefore expected to be more vulnerable than sable antelope to natural predation.

Browsers such as greater kudu are less dependent on surface-water than grazers like sable antelope, and mixed-feeders like impala (Western, 1975). As the dry season advances, grazers and mixed-feeders are compelled to forage farther from waterholes to mitigate limitations in nutritional requirements (Redfern et al., 2003). Sable antelopes, in particular, travel longer distances between waterholes and feeding sites in the dry season, which may increase their energy expenditure and exposure to predators (Rahimi et Owen-Smith, 2007). Thus, sable antelopes should me more constrained by surface-water than greater kudu, and impala to a lower extent.

Harvest rates are traditionally set at ca. 2% of population size for most ungulates in Zimbabwean hunting areas (Cumming, 1989), and the perceived hunting risk was comparable among the three ungulate species (Crosmary et al., 2012). For sable antelope, however, only males were hunted, while females were also allocated for greater kudu and impala. The magnitude of behavioural adjustments to hunting risk should therefore vary among our three biological models mainly according to contrasted vulnerability to predation and constraints on surface-water (Table 3.1).

Behavioural monitoring

We monitored the behaviour of ungulates in the vicinity of 31 waterholes (18 in HNP, 13 in HA) (Fig. 3.1). We selected waterholes according to the availability of surface-water and signs of recent ungulates presence, i.e. fresh spoors and faeces. We used binoculars (10X42) to conduct behavioural observations during daytime (i.e. from 06.00h to 18.00h), from viewing platforms, a hide on the ground, or a car parked at ca. 100 to 150 m away from waterholes in order not to disturb animals. Because the studied species are gregarious and previous studies have shown that they adjusted their behaviour both at the group and the individual levels (e.g. Valeix et al., 2007; Périquet et al., 2010), we performed behavioural observations both on groups and individuals.

Monitoring of individuals

We monitored individuals during i) the approach, which corresponds to the period from the moment the individual appears in the waterhole area (i.e. the open area around a waterhole) to the moment it starts drinking, ii) the drinking, i.e. the period from the moment the individual starts drinking to the moment it stops drinking (includes all drinking and vigilance bouts), and iii) the departure, the period from the moment the individual stops drinking to the moment it has left the waterhole area. We considered these three phases separately because vigilance may be unevenly distributed during the different phases (Périquet et al., 2010).

Table 3.1: Comparisons of vulnerability to predation and constraints on surface-water for three ungulate species, impala, greater kudu, and sable antelope in Hwange National Park and the surrounding hunting concessions, Zimbabwe. The expected behavioural adjustments around waterholes (i.e. time spent in vigilance and drinking probability) are compared among species, as well as the predicted response to hunting risk in hunting concessions (i.e. further increase of time spent in vigilance, further decrease of drinking probability).

	Species		
	Impala	Greater kudu	Sable antelope
Vulnerability to predation	++	+++	+
Surface-water constraint	++	+	+++
Time spent in vigilance	++	+++	+
Drinking probability	++	+	+++
Response to hunting risk	++	+	+

The ‘+’ ranks the species, i.e. more ‘+’ ranks first, and less ‘+’ ranks last.

During each phase, we performed 2-minute focal observations to monitor the behaviour of adult individuals within groups. The duration of focal observations was limited by the high turnover of groups around waterholes. These 2-minute focal observations were, however, sufficient to capture several behavioural bouts (i.e. average number of behavioural bouts in two minutes for the three species: 12 ± 5 during approach, 15 ± 5 during drinking, and 20 ± 9 during departure), which allowed us to test for behavioural differences between HNP and HA. During the 2-min focal observations, we measured the time individuals spent in i) vigilance, ii) drinking while in the drinking phase, and iii) walking while approaching or leaving the waterhole. Vigilance was clearly distinct from other behaviours, with vigilant animals typically standing and raising their head above the shoulders with ears holding forward (Alados, 1985). During our observations, focal animals did not stand without being vigilant, so we considered standing bouts as vigilance bouts. These behaviours were exclusive from one another, as the time an individual spent in vigilance was negatively correlated with time spent walking or drinking (Appendix 3.1). We also recorded the total duration of the drinking phase of focal individuals. We recorded the sex of focal individuals, group size, presence of young in the group (yes/no), and the minimal distance to vegetation cover (measured with a rangefinder as the distance from the waterhole to the closest scrub/tree line), because these factors may influence the perception of predation risk (e.g. Dehn, 1990; Burger et Gochfeld, 1994; Burger et al., 2000).

Monitoring of groups

For each group entering the waterhole area, we recorded whether the group drank (i.e. at least one individual drank) or not (i.e. none of the individuals drank). When the group drank, we measured the group i) approach time, i.e. the period from the moment the group enters the waterhole area to the moment the first individual of the group begins to drink, ii) drinking time, i.e. the period from the moment the first individual of the group begins to drink to the moment the last individual of the group stops drinking, and iii) departure time, i.e. the period from the moment the last individual of the group stops drinking to the moment the group has left the waterhole area. Distances walked by groups in approach and departure phases may influence the group approach and departure times. We therefore recorded the approach and departure distances in categories (i.e. 0-50m, 50-100m, 100-150m, 150-200m, >200m) for each group, and accounted for this in the analyses.

The study comprised 84 days of observations in HNP (ca. 1 000h), and 46 in HA (ca. 550h). We observed 268 groups in HNP (133 of impala, 120 of greater kudu, and 15 of sable antelope), and 226 groups in HA (134 of impala, 54 of greater kudu, and 38 of sable antelope). We obtained a total of 154 individual focal observations in HNP (52 for impala, 60 for greater kudu, and 42 for sable antelope), and 166 in HA (68 for impala, 58 for greater kudu, and 40 for sable antelope). Group size ranged from 1 to 110 in impala (mean

± sd = 10 ± 14), 1 to 20 in greater kudu (mean ± sd = 5 ± 4), and 1 to 50 in sable antelope (mean ± sd = 10 ± 12).

Statistical analyses

Drinking probability

We used mixed logistic regressions to calculate the probability of drinking once animals had entered the waterhole area. We tested the effect of land use, i.e. HNP (no hunting) vs HA (hunting). We included presence of young in the group, group size, and minimal distance to vegetation cover as covariates. We added waterholes identity as random factor. We then compared the probability of drinking among species by running logistic models for each land use separately, with species as a single factor.

Individual behaviour

For each species, we first computed the proportion of time spent in vigilance by single individuals during the 2-min focals in each phase, and the total duration of their drinking phase. We arcsine square root-transformed these proportions, and square root-transformed the total durations of the drinking phase to meet assumptions of normality and homogeneity of variance (Sokal et Rohlf, 1995). We used linear mixed models, with waterhole identity as random factor, to test the effect of land use on the proportion of time individuals spent in vigilance, and on the total duration of individual drinking phase. In addition of land use, we tested the effect of presence of young, sex, group size, and minimal distance to vegetation cover as covariates. We then used linear models to test for the effects of phase and species, and their interaction, on the proportion of time individuals spent in vigilance.

Group approach, drinking, and departure times

The time spent in the different phases by groups was log-transformed to meet the assumptions of normality and homogeneity of variance. For the approach and departure phases, we used linear mixed models with approach and departure distances, and waterhole identity as random factors to test for the effect of land use. For the drinking phase, we used linear mixed models with waterhole identity as random factor. In each case, we also tested for the effects of presence of young, group size, and minimal distance to vegetation cover as covariates.

For the selection of models, we used the Akaike Information Criterion (AIC) to select the best model with the small sample adjustment AICc (Burnham et Anderson, 2002). The model with the lowest AICc value (i.e. the best compromise between accuracy and precision) was retained. When ΔAICc between two models was less than two, we selected the simplest model according to the parsimony rules (Burnham et Anderson, 2002). We defined a set of a priori models for each species and each dependant variable (Appendix 3.2). Statistical analyses were performed with R *nlme* and *lme4* packages for linear and generalized linear mixed models (http://cran.r-project.org/web/packages/index.html).

Results

Drinking probability

The selected model for the probability of drinking in impala included land use, minimal distance to vegetation cover, and their interaction (Appendix 3.2). The probability of drinking was lower in HA compared to HNP (Table 3.2). This probability decreased as the minimal distance to vegetation cover increased, but less rapidly in HA (Table 3.2). For greater kudu, the model selected only included group size (Appendix 3.2), the probability of drinking increasing with group size (Table 3.2). In sable antelope, land use and the covariates did not influence the probability of drinking (Table 3.2, Appendix 3.2).

In HNP, the drinking probability of groups was lower for greater kudu than for impala (ca. 83% *vs* 93% respectively; estimate ± SE = -1 ± 0.4, $Z_{1,\,273} = -2.4$, $P = 0.02$), whereas we observed no difference between sable antelope and impala (ca. 94% and 93% respectively; $Z_{1,\,273} = 0.1$, $P = 0.9$). In HA however, this probability was higher for groups of sable antelope compared to groups of impala (ca. 95% *vs* 76% respectively; estimate ± SE = -1.8 ± 0.8, $Z_{1,\,241} = -2.4$, $P = 0.02$), and to groups of greater kudu (ca. 95% *vs* 67%

respectively; estimate ± SE = -2.2 ± 0.8, $Z_{1,\ 241}$ = -2.9, P = 0.004), whereas there was no significant difference between impala and greater kudu ($Z_{1,\ 241}$ = -1.6, P = 0.1).

Individual level

Approach phase

For the three species, the selected model for the proportion of time in vigilance during approach only included land use (Appendix 3.2). The proportion of time individuals spent in vigilance while they were approaching waterholes was respectively 2.5, 1.5, and 3.7 times higher in HA than in HNP for impala, greater kudu, and sable antelope (Table 3.3, Fig. 3.2a).

Drinking phase

The selected model for the proportion of time in vigilance during drinking only included land use for impala, whereas none of the variables influenced this proportion in greater kudu and sable antelope (Appendix 3.2). Impala were 1.7 times more vigilant in HA than in HNP while drinking, whereas there was no difference for greater kudu and sable antelope (Table 3.3, Fig. 3.2b).

The total duration of the individual drinking phase did not differ between HA and HNP for all species (impala: $F_{1,\ 62}$ = 2.4, P = 0.1; greater kudu: $F_{1,\ 43}$ = 3.4, P = 0.07; sable antelope: $F_{1,\ 38}$ = 3.6, P = 0.07).

Departure phase

The selected model for the proportion of time in vigilance during departure only included land use for impala and sable antelope, whereas none of the variables influenced this proportion for greater kudu (Appendix 3.2). Impala and sable antelope were respectively 1.8 and 1.3 times more vigilant in HA than in HNP while leaving waterholes, whereas there was no difference for greater kudu (Table 3.3, Fig. 3.2c).

Effects of species and phase on the time individuals spent vigilant

The phase influenced the proportion of time individuals spent in vigilance in HNP ($F_{2,\,168}$ = 28.2, $P < 0.0001$) (Fig. 3.3a) and in HA ($F_{2,\,193}$ = 103.5, $P < 0.0001$) (Fig. 3b). In both land uses, individuals of the three species were less vigilant while drinking than while approaching (in HNP: estimate ± SE = -0.1 ± 0.07, $t_{1,\,168}$ = -2, P = 0.05; in HA: estimate ± SE = -0.4 ± 0.06, $t_{1,\,193}$ = -7.1, $P < 0.0001$) and leaving (in HNP: estimate ± SE = -0.3 ± 0.07, $t_{1,\,168}$ = -4.6, $P < 0.0001$; in HA: estimate ± SE = -0.4 ± 0.06, $t_{1,\,193}$ = -7.6, $P < 0.0001$) waterholes.

In HNP, the proportion of time individuals spent in vigilance differed with species ($F_{2,\,168}$ = 14.2, $P < 0.0001$). Greater kudu were more vigilant than impala (estimate ± SE = 0.2 ± 0.08, $t_{1,\,168}$ = 2.7, P = 0.008), whereas we observed no difference between sable antelope and impala ($t_{1,\,168}$ = -0.5, P = 0.6). In HA conversely, time individuals spent vigilant did no vary with species ($F_{2,\,193}$ = 1.3, P = 0.3). The interaction between phase and species was non significant in HNP ($F_{4,\,168}$ = 0.8, P = 0.5) and in HA ($F_{4,\,193}$ = 1.7, P = 0.1).

Group approach, drinking, and departure times

Approach time

The null models were selected for the three species, meaning that the time for groups to approach waterholes was neither influenced by land use, nor by the covariates (Fig. 3.4a, Table 3.4, Appendix 3.2).

Drinking time

For the three species, land use was not included in the selected models, meaning that this variable had no effect on the drinking time of groups (Fig. 3.4b, Table 3.4, Appendix 3.2). This time however increased with group size in impala (Table 3.4), and was shorter for groups without juveniles in greater kudu (Table 3.4).

Table 3.2: Estimated parameters and their 95% confidence intervals for the most parsimonious models of drinking probability of groups, for impala, greater kudu, and sable antelope, in approach, drinking, and departure at waterhole areas, in Hwange National Park (HNP, non-hunting area) and the peripheral hunting areas (HA), Zimbabwe, during the 2008 dry season.

Drinking probability	Selected model	k[a]	Parameter	df	Estimate	[CI95%]
Impala	land use X distance to cover	18	Intercept	1	6.17	[3.25, 9.09]
			HA[b]	1	–4.59	[–7.92, –1.25]
			distance to cover	1	–0.06	[–0.09, –0.02]
			HA X distance to cover	1	0.05	[0.01, 0.1]
Greater kudu	group size	15	Intercept	1	0.67	[–0.19, 1.55]
			group size	1	0.15	[0.02, 0.29]
Sable antelope	null	12	Intercept	1	9.04	[–4.21, 22.3]

[a] Number of parameters. It includes the random factor “waterholes”.

[b] Results are presented as the difference estimate between the “HA” and the reference class “HNP”.

Table 3.3: Estimated parameters and their 95% confidence intervals for the most parsimonious models of proportion of time individuals spent in vigilance, for impala, greater kudu, and sable antelope, in approach, drinking, and departure at waterhole areas, in Hwange National Park (HNP, non-hunting area) and the peripheral hunting areas (HA), Zimbabwe, during the 2008 dry season.

Individual vigilance[a]	Species	Selected model	k[b]	Parameter	df	Estimate	[CI95%]
Approach	Impala	land use	9	Intercept	1	0.44	[0.28, 0.60]
				HA[c]	1	0.42	[0.20, 0.65]
	Greater kudu	land use	9	Intercept	1	0.64	[0.74, 0.55]
				HA	1	0.24	[0.09, 0.39]
	Sable antelope	land use	9	Intercept	1	0.40	[0.22, 0.59]
				HA	1	0.42	[0.15, 0.69]
Drinking	Impala	land use	9	Intercept	1	0.26	[0.37, 0.15]
				HA	1	0.18	[0.08, 0.29]
	Greater kudu	null	9	Intercept	1	0.53	[0.47, 0.59]
	Sable antelope	null	9	Intercept	1	0.31	[0.22, 0.39]
Departure	Impala	land use	9	Intercept	1	0.58	[0.46, 0.71]
				HA	1	0.32	[0.15, 0.50]
	Greater kudu	null	11	Intercept	1	0.85	[0.75, 0.95]
	Sable antelope	land use	9	Intercept	1	0.73	[0.60, 0.85]
				HA	1	0.25	[0.07, 0.43]

[a] Proportion of time spent in vigilance (arcsine square root-transformed data) over the 2-minute focals.

[b] Number of parameters. It includes the random factor “waterholes”.

[c] Results are presented as the difference estimate between the “HA” and the reference class “HNP”.

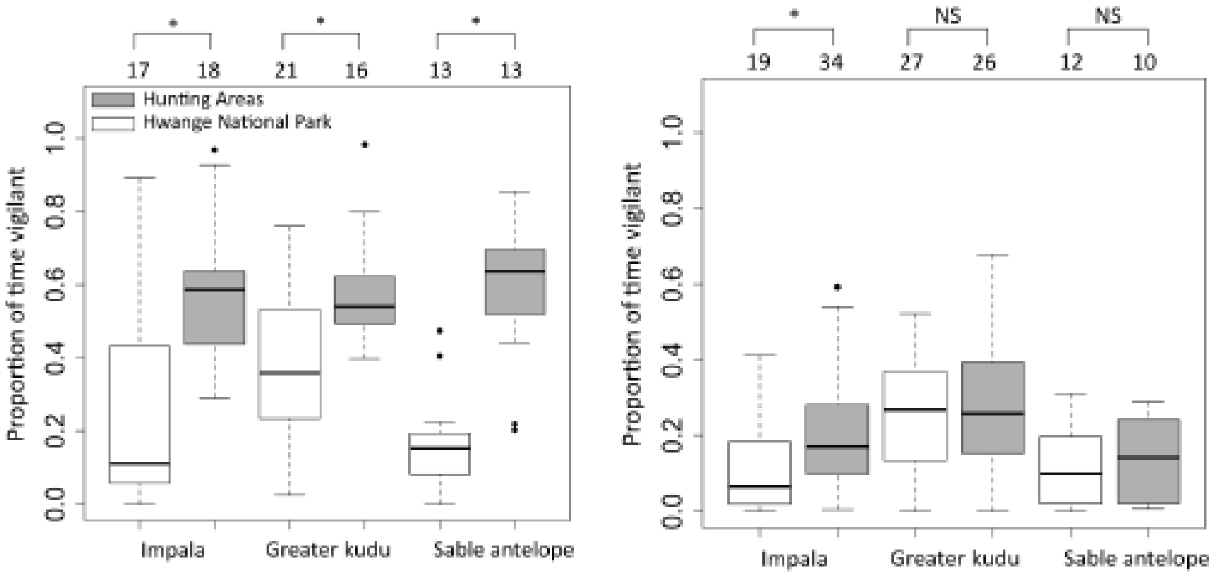
Table 3.4: Estimated parameters and their 95% confidence intervals for the most parsimonious models of time groups spent in approach, drinking, and departure at waterhole areas, for impala, greater kudu, and sable antelope, in Hwange National Park (HNP, non-hunting area) and the peripheral hunting areas (HA), Zimbabwe, during the 2008 dry season.

Group time[a]	Species	Selected model	k[b]	Parameter	df	Estimate	[CI95%]
Approach	Impala	null	24	Intercept	1	1.31	[1.06, 1.56]
	Greater kudu	null	31	Intercept	1	1.51	[1.08, 1.95]
	Sable antelope	null	16	Intercept	1	1.57	[1.15, 2.00]
Drinking	Impala	group size	14	Intercept	1	1.49	[1.30, 1.67]
				group size	1	0.025	[0.019, 0.032]
	Greater kudu	status	17	Intercept	1	2.01	[1.83, 2.18]
				no juvenile[c]	1	–0.31	[–0.52, –0.10]
	Sable antelope	null	10	Intercept	1	1.77	[1.51, 2.03]
Departure	Impala	null	27	Intercept	1	1.64	[1.32, 1.96]
	Greater kudu	status	19	Intercept	1	1.76	[1.43, 2.09]
				no juvenile	1	–0.47	[–0.81, –0.13]
	Sable antelope	null	16	Intercept	1	1.74	[1.47, 2.02]

[a] Log transformed data.

[b] Number of parameters. It includes the random factors “waterholes”, and “approach distance” or “departure distance” for the approach and departure phases.

[c] Results are presented as the difference estimate between the “no juvenile” and the reference class “presence of juveniles.



a) during approach

b) during drinking

c) during departure

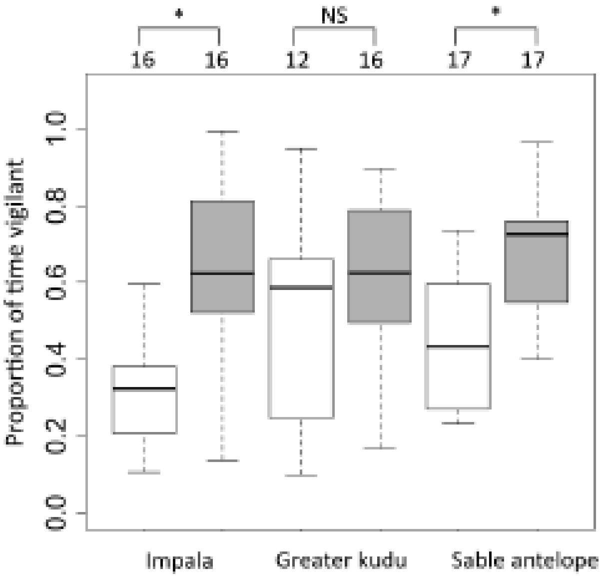
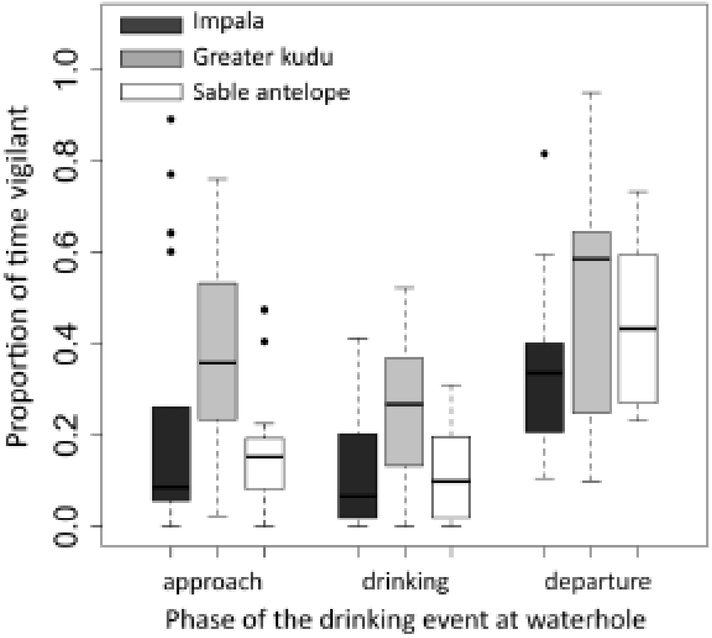


Figure 3.2: Proportion of time individuals spent in vigilance during the a) approach, b) drinking, and c) departure phases while using waterholes for impala, greater kudu, and sable antelope, in Hwange National Park (hunting-free area) *vs* the adjacent sport hunting areas. * $P < 0.05$. NS= non-significant. Sample sizes are given above each box plot. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentiles, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are the observation <10th or >90th percentiles.

a) in Hwange National Park



b) in sport hunting areas

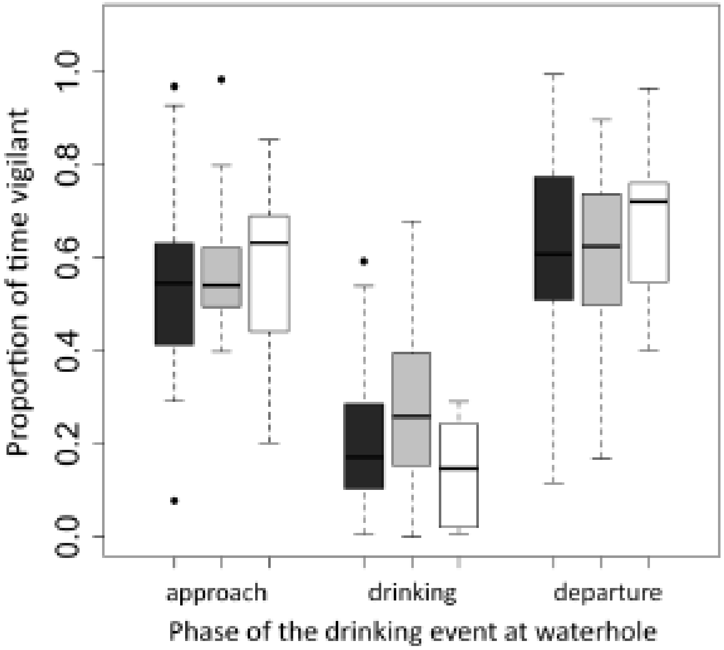
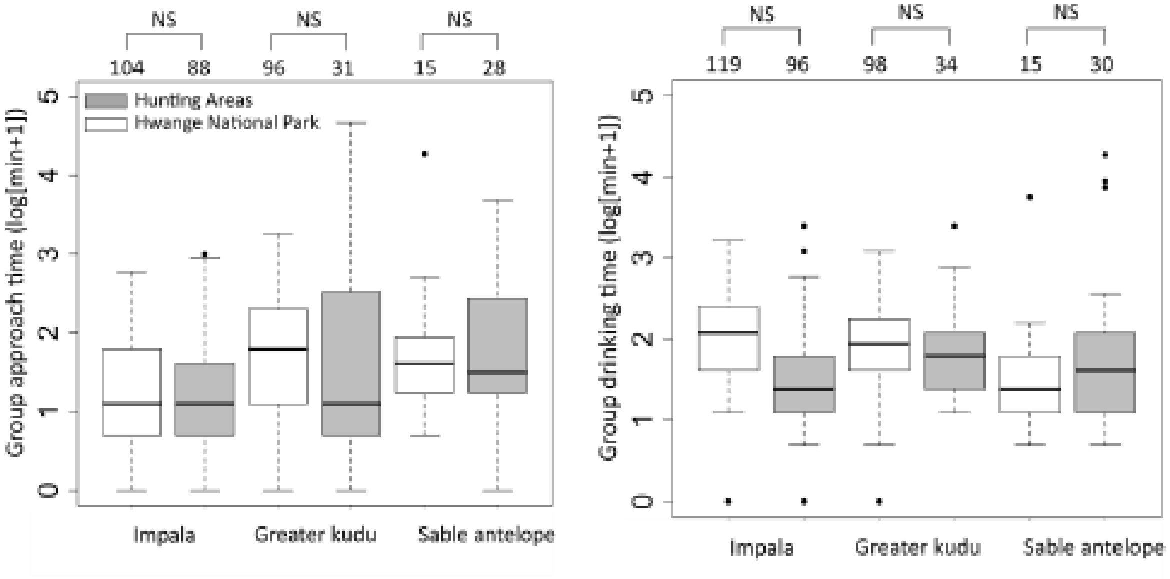


Figure 3.3: Proportion of time individuals spent in vigilance during all phases at waterholes for impala, greater kudu, and sable antelope in a) Hwange National Park (hunting-free area), and in b) adjacent sport hunting areas. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentiles, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are the observation <10th or >90th percentiles.



a) during approach

b) during drinking

c) during departure

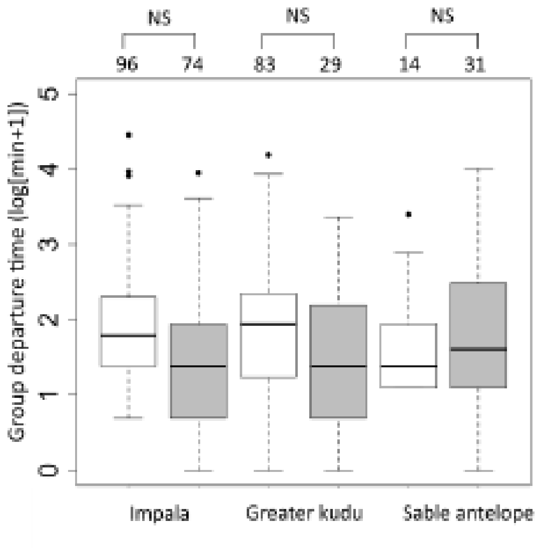


Figure 3.4: Time groups spent in a) approach, b) drinking, and c) departure phases while using waterholes for impala, greater kudu, and sable antelope, in Hwange National Park (hunting-free area) *vs* the adjacent sport hunting areas. * *P* < 0.05. NS= non-significant. Sample sizes are given above each box plot. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentiles, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are the observation <10th or >90th percentiles..

Departure time

For the three species, land use was not included in the selected models, meaning that this variable had no effect on the departure time of groups (Fig. 3.4c, Appendix 3.2). This time was however shorter for groups without juveniles in greater kudu (Table 3.4).

Discussion

Behavioural adjustments in response to hunting risk have been outlined in several large herbivores (e.g. Kilgo et al., 1998; Aastrup, 2000; Matson et al., 2005; Setsaas et al., 2007; Reimers et Colman, 2006; Benhaiem et al., 2008). However, the extent to which large herbivores can adjust their behaviour in response to both hunting and predation risks remains poorly understood, because most studies have concentrated on northern ecosystems where human activities have widely reduced the diversity and densities of natural predators, hence predation risk for large herbivores (Berger, 1999).

In Hwange National Park (hunting-free area), Zimbabwe, more than 90% of the groups of impala and sable antelope, and nearly 85% of the groups of greater kudu eventually drank once they had entered waterhole areas. This suggests that most large African herbivores depend on surface water (Western, 1975; Thrash et al., 1995; Owen-Smith, 1996; Redfern et al., 2003). It also shows that greater kudu is more likely to leave waterholes without drinking, possibly as a result of the combined effect of its greater vulnerability to natural predators and its lower dependence on surface-water. In the neighbouring hunting areas, however, up to 24% of groups of impala and 33% of groups of greater kudu left waterhole areas without drinking. Groups of sable antelope, conversely, showed no decrease of drinking probability in hunting areas compared to the National Park. This is consistent with the observation that sable antelope is more constrained by surface water than greater kudu and impala (Redfern, 2003; Rahimi et Owen-Smith, 2007). Animals more constrained by resource requirements are indeed less likely to adjust their behaviour in response to disturbance (Gill et al., 2001; Beale et Monaghan, 2004).

Results at the individual level clearly showed, however, that sable antelope, like impala and greater kudu, behaviourally responded to hunting risk. In groups that eventually approached waterholes to drink, individuals spent more time in vigilance in hunting areas compared to the National Park for all species. Greater kudu was the most vulnerable species to natural predation in our study (Loveridge et al., 2007; Drouet-Hoguet, 2007), and was accordingly the most vigilant in the National Park. As predicted, greater kudu displayed the lowest increase of vigilance in response to hunting risk. Indeed, vigilance overall increased by 32% in greater kudu (from 34% in HNP to 45% in HA), compared to 65% (from 20% to 33%) and 85% (from 27% to 50%) for impala and sable antelope respectively. Périquet et al. (2010) previously suggested that greater kudu were already close to a maximum level of vigilance in Hwange national Park, and could therefore hardly increase further their vigilance in response to extra risk. The time allocated to vigilance is indeed limited because the costs associated with an increase of vigilance may eventually outweigh the benefits of reduced risk (Lima et Dill, 1990; Lima, 1998). Feeding rate for instance is reduced as vigilance increases (Beauchamp et Livoreil, 1997; Fritz et al., 2002). In our study, vigilance increased at the expense of walking and drinking. Increased vigilance may thus force individuals to extend their stay in waterhole areas, away from shade and protective cover, and so may alter thermoregulation (e.g. Jarman et Jarman, 1973; Owen-Smith, 1998), and increase exposure to natural predators (Valeix et al., 2007).

Vigilance varied according to the main activity individuals were engaged in. For the three species, individuals were indeed more vigilant while they were approaching or leaving waterholes, than while they were drinking. They thus prioritized drinking over vigilance once they had reached waterholes, despite drinking being the riskiest period because this is when animals are the furthest away from protective cover. In hunting areas, moreover, vigilance greatly increased during approach and departure, whereas it did not vary much during drinking. By not increasing their vigilance during drinking, individuals managed to satisfy their water requirements without extending their drinking period, and thus the time they remained exposed to predators and hunters. Vigilance during foraging periods is limited (Illius et FitzGibbon, 1994; Shipley et al., 1999; Cowlishaw et al., 2004). Interestingly, only impala increased vigilance during drinking in response to hunting. This supported our prediction that species less vulnerable to natural predators and less constrained by key resources are more likely to adjust further their behaviour in response to hunting because they have the capacity to do so.

At the group level, the increase in individual vigilance should have resulted in extended periods spent in waterhole areas. Groups in hunting areas, however, approached, drank, and left waterholes as fast as groups in the National Park. This indicates that groups in hunting areas were more cohesive than groups in the National Park, i.e. distances among group members were reduced (e.g. Lingle, 2001). Enhanced cohesion would therefore allow groups in hunting areas to reduce time spent in waterhole areas, thus limiting their exposure to hunters. Greater cohesion in groups moreover promotes the dilution effect (Hamilton, 1971; Dehn, 1990), and increases confusion in predators (Neill et Cullen, 1974; Milinski, 1977). It however requires greater synchrony in behaviours among group members. Such synchrony may be costly for individuals because they have to compromise their own activity budgets to follow the behaviour of other group members (e.g. Côté et al., 1997; reviewed in Conradt et Roper, 2005).

Group size positively influenced drinking probability in greater kudu. The risk perceived by individuals decreases in larger groups because of dilution (Hamilton, 1971; Dehn, 1990), and that there are more eyes to detect danger (‘many eyes’ effect, Pulliam, 1973). Drinking probability, however, did not increase with group size in impala and sable antelope, possibly because these species form larger groups than greater kudu, and that the effect of increased group size was negligible in larger groups. The time groups spent drinking increased with group size in impala, probably because the more individuals, the longer it took for groups to complete the drinking phase. In approach and departure phases, however, there was no effect of group size. We suspect that larger groups managed to limit the duration of approach and departure, and thus the time spent in waterholes areas, by increasing their cohesion. This, however, remains to be investigated.

Sex did not influence time individuals spent vigilant, whereas we could have expected males to be more vigilant than females in hunting areas (e.g. Matson et al., 2005), because hunting is male-biased in sable antelope, and in greater kudu to a lower extent. Hunters frequently target males in mixed groups (ZPWMA, personal observations), thus females are often disturbed as much as males. Presence of young in groups had no effect on individual vigilance. At the time of the study young were ca. 10 months old, and so less vulnerable to predators than earlier in the year (Bourgarel, 2004). Risk perceived in groups with young was therefore possibly not higher than in groups without young. However, the time groups spent in drinking and departure was shorter in absence of juveniles in greater kudu. As the minimal distance to vegetation cover increased, drinking probability decreased. This is consistent with previous studies highlighting that the risk perceived increased with distance to protective cover (Creel et Winning, 2005; Valeix et al., 2007). The absence of such effects in greater kudu is consistent with the suggestion that greater kudu are close to a maximum level of vigilance, and cannot increase further their vigilance (Périquet et al., 2010). Likewise for sable antelope that are less likely to adjust their vigilance at waterholes because of higher constraint on access to surface water compared to greater kudu and impala (Western, 1975; Redfern et al., 2003; Rahimi et Owen-Smith, 2007).

Conclusion

Our study illustrates how both vulnerability to natural predation and resource requirements constrain the behavioural adjustments of prey species to hunting risk. Species that naturally display strong adjustments in response to predation risk such as greater kudu, and species that are strongly constrained by resource requirements such as sable antelope are less likely to adjust their behaviour in response to the extra risk imposed by hunting. This challenges the risk-disturbance hypothesis that predicts that prey species that naturally experience higher predation risk are more likely to respond to human disturbance (Frid et Dill, 2002). Our work, moreover, illustrates how changes in behaviour may not always be good measures of the relative susceptibility of species to human disturbance (Gill et al., 2001), and urges for the importance of multi-species studies in the investigation of wildlife responses to human disturbance (Blumstein et al., 2005). In terms of management and conservation, further research is needed on the associated costs of behavioural adjustments in response to hunting risk, e.g. alteration of activity budgets, costs of synchrony, and increased exposure to natural predators. This would help managers deciding whether the design of ‘hunting-free sanctuary zones’ around key resources, such as waterholes in semi-arid African savannas, is desirable in hunting areas.

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Partie II

Effets directs de la chasse aux trophées: la taille des cornes, la proportion de mâles adultes, et les densités de population

CHAPITRE 4
30 ANNÉES DE TROPHÉES: DES CORNES PLUS PETITES?

Trophy hunting in Africa: long-term trends in antelope horn size

WILLIAM-GEORGES CROSMARY, ANDREW J. LOVERIDGE, HENRY NDAIMANI, SÉBASTIEN LEBEL, VERNON BOOTH, STEEVE D. CÔTÉ, HERVÉ FRITZ

Résumé

Le prélèvement sur des critères de taille comme la chasse aux trophées peut favoriser les individus qui investissent plus tôt dans la reproduction au détriment de la croissance, et ainsi induire des changements morphologiques vers des individus aux traits plus petits. Un déclin de la taille des trophées (e.g. corne/bois) risque d'altérer la viabilité des populations chassées, et de compromettre le rôle de conservation des zones de chasse. C'est une question majeure en Afrique, parce que les zones de chasse représentent plus de la moitié de la superficie totale des aires protégées. Nous avons examiné la tendance de la longueur des cornes des mâles prélevés chez l'impala (*Aepyceros melampus*), le grand koudou (*Tragelaphus strepsiceros*), et l'hippotrague noir (*Hippotragus niger*), de 1974 à 2008 à *Matetsi Safari Area*, Zimbabwe. La longueur des cornes a décliné de quatre pourcents chez l'impala, mais principalement parce que les mâles prélevés étaient de plus en plus jeunes. Chez le grand koudou, la longueur des cornes a augmenté de 14 pourcents, vraisemblablement parce que la pression de chasse a diminué chez cette espèce au cours de la période d'étude, ce qui a probablement permis aux mâles de vivre plus vieux et de développer des cornes plus longues avant d'être prélevés. La longueur des cornes a décliné de six pourcents chez l'hippotrague noir, indépendamment de l'âge, suggérant que la chasse aux trophées a promu au fil des années la contribution reproductive des mâles à la croissance de cornes lente, en supposant que la longueur des cornes soit héritable. La pression de chasse et la valeur du trophée étaient plus élevées chez l'hippotrague noir que chez l'impala et le grand koudou. En conséquence, le déclin de la longueur des cornes était plus prononcé chez l'hippotrague noir. Abaisser la pression de chasse sur cette espèce pourrait ne pas être suffisant pour mitiger le déclin observé dans la longueur des cornes.

Abstract

Size-selective harvesting such as trophy hunting may favour individuals that invest early in reproduction to the detriment of growth, and therefore induce morphological changes towards individuals with smaller traits. A decrease in trophy size (e.g. horn/antler size) may alter the viability of harvested populations, and jeopardize the conservation potential of hunting areas. This would be a major concern in Africa where hunting zones represent over half of the total area of protected lands. We investigated horn length trends of harvested males in impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and sable antelope (*Hippotragus niger*), from 1974 to 2008 in Matetsi Safari Area, Zimbabwe. Horn length declined of four percents in impala, but mainly because males were harvested increasingly younger. In greater kudu, horn length surprisingly increased of 14 percents. This likely resulted from reduced hunting pressure on this species during the same period, which may have allowed males to live older and to grow longer horns before being harvested. Horn length declined of six percent in sable antelope, independent of age, suggesting that trophy hunting promoted the reproductive contribution of males with slow-growing horns through time, provided horn length is heritable. Hunting pressure and trophy value were higher in sable antelope compared to impala and greater kudu. Accordingly, the decline of horn length in this species was more pronounced. A release of hunting pressure on this species may not be sufficient to reverse the decline observed in horn length.

Keywords: selective harvest, trophy hunting, African ungulates, horn size, Zimbabwe

Introduction

Size-selective harvesting increases the mortality of large individuals, and may therefore select for individuals that invest early in reproduction to the detriment of somatic growth and adult body size. Whereas the potential evolutionary consequences of size-selective harvesting regimes have been well documented in fisheries (e.g. Sutherland, 1990; Browman, 2000; Conover et Munch, 2002), empirical studies in ungulates hunted for trophy traits, i.e. horn/antler size, are still rare (but see Coltman et al., 2003; Garel et al., 2007). In polygynous species such as many ungulates, sexual selection favours males with rapid early growth and investment in structural size at the expense of early sexual maturity (Trivers, 1972; Clutton-Brock, 1988). Male ungulates have thus evolved horns or antlers that are large with complex shapes through sexual selection (Geist, 1966; Packer, 1983; Caro et al., 2003). By selecting males with the largest trophy traits, hunters may induce morphological change within the population by artificially selecting for individuals with smaller sexually selected traits, e.g. shorter or thinner horns (Coltman et al., 2003; Garel et al., 2007). Ultimately, there may be biological drawbacks to smaller horns because this trait could reduce individual fitness (Hartl et al., 2003), or be associated with lower genetic variability (Scribner et al., 1989; Fitzsimmons et al., 1995).

Worldwide, trophy hunting is a popular and lucrative activity (Lindsey et al., 2007b; Frisina et Tareen, 2009; Sharp et Wollscheid, 2009). It gives substantial economic value to wildlife, and therefore creates incentives for the preservation of natural habitats of trophy species, particularly in developing countries (Loveridge et al., 2007b). The sustainability of trophy hunting as an efficient conservation tool, however, depends on the presence of large trophy animals (i.e. large horned/antlered males) to satisfy hunter client expectations (Festa-Bianchet, 2007). Consequently, a decrease in trophy size may not only be detrimental to the viability of the harvested population (Hartl et al., 2003; Coltman et al., 2005), but also for the sustainability of trophy hunting as a conservation tool.

Growth and development of horns and antlers may also be influenced by factors affecting resource quality and availability. For instance, males develop smaller body weight, and grow shorter horns or antlers at higher densities because of density-dependent competition (Jorgenson et al., 1998; Festa-Bianchet et al., 2004; Schmidt et al., 2007).

Likewise, shorter horns and antlers have been observed in harvested populations when environmental conditions deteriorate, e.g. loss of suitable habitat (Garel et al., 2007) or intensity of droughts (Torres-Porras et al., 2009). Finally, the proximity of a hunting-free source area from which males disperse could theoretically counteract the selective process induced by trophy hunting, and mitigate change towards smaller trophy size in hunting areas (Tenhumberg et al., 2004). The distance from a hunting-free area could therefore influence both the spatial pattern and the temporal trend of trophy size in hunting areas.

Although trophy hunting is a particularly well-developed industry in African savannas (Lindsey et al., 2007a, b), trends in horn size have been little studied in African ungulates. Only von Brandis and Reilly (2007, 2008) have previously reported on horn size trends of African ungulates, in South Africa. However, as these authors mentioned, hunting in South Africa occurs on small and fenced private ranches where trophy quality is managed and manipulated, and is therefore not representative of trophy hunting over much of Africa. The richness of the African ungulate guild offers a unique opportunity to compare the effects of size-selective harvest on different species within the same ecosystem. Species may indeed respond in different ways to trophy hunting, depending on hunting pressure (i.e. number of adult males harvested / number of adult males in the hunted population), and species trophy value to hunters (i.e. cost of a hunting safari).

Here, we investigated the temporal and spatial trends in horn size for different African ungulates over three decades in the Matetsi Safari Area, a complex of hunting areas adjacent to Hwange, Kazuma Pan, and Zambezi National Parks (i.e. hunting-free protected areas), Zimbabwe. The country is one of the most popular destinations for hunting tourism in Sub-Saharan Africa (Lindsey et al., 2006). The Zimbabwean hunting industry has generated up to about 16 million US Dollars of revenue per year for the past few decades, and encompasses ca. 70,000km^2 of lands; a total of 17% of Zimbabwe's land surface (Cumming, 1999; Booth, 2002). We hypothesised that trophy hunting impacted horn size of antelopes and thus 1) we generally expected horn size to decline over time for all species, and more particularly, 2) we expected the decline of horn size to be more pronounced for species with higher hunting pressure and trophy value. If the national parks acted as a source of large-horned males, 3) we expected horn size to be on average smaller, and to decline more rapidly over the years as the distance from the national parks increased. With regard to potential long-term changes in the abundance of the large herbivores community, 4) we expected that horn size would decline with increasing abundance of competitors through reductions in forage availability.

Methods

Study area

Matetsi Safari Area (MSA), ca. 3,000 km^2, is one of the largest hunting complexes of Zimbabwe. It stretches along the unfenced northern boundary of Hwange National Park (HNP, hunting-free area), ca. 15,000 km^2, up to the Zambian border (Fig. 4.1). MSA is a state land administered by Zimbabwe Parks and Wildlife Management Authority (ZPWMA), but leased to safari operators. Hunting tourism officially started in the area in 1973, but expanding significantly in the mid-1980s (ZPWMA, personal communication). MSA is divided into seven hunting units, units one to five in the southern part, units six and seven in the northern part. We removed units six and seven from our study because unit seven ceased to be a hunting area in 1995, and because vegetation types and environmental conditions (i.e. rainfall, temperature, soil characteristics) in these two units differ from the five units of the southern part (Ganzin et al., 2008; Peace Parks Foundation, 2009). We thus concentrated our study on units one to five (404 km^2, 292 km^2, 356 km^2, 470 km^2, and 370 km^2 respectively). These units are located on well-drained shallow rocky soils, where vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of grasslands, and dominance of *Colophospermum mopane* and *Combretum spp.* (Rogers, 1993; Ganzin et al., 2008). Communal and private lands border the eastern part of the complex, and the western part of units three and two. Unit one is bordered by Kazuma Pan National Park (KPNP, ca. 310 km^2) and by two hunting areas managed by the Forestry Commission (i.e. Kazuma and Panda-Masuie Forests) at the western and northern limits (Fig. 4.1).

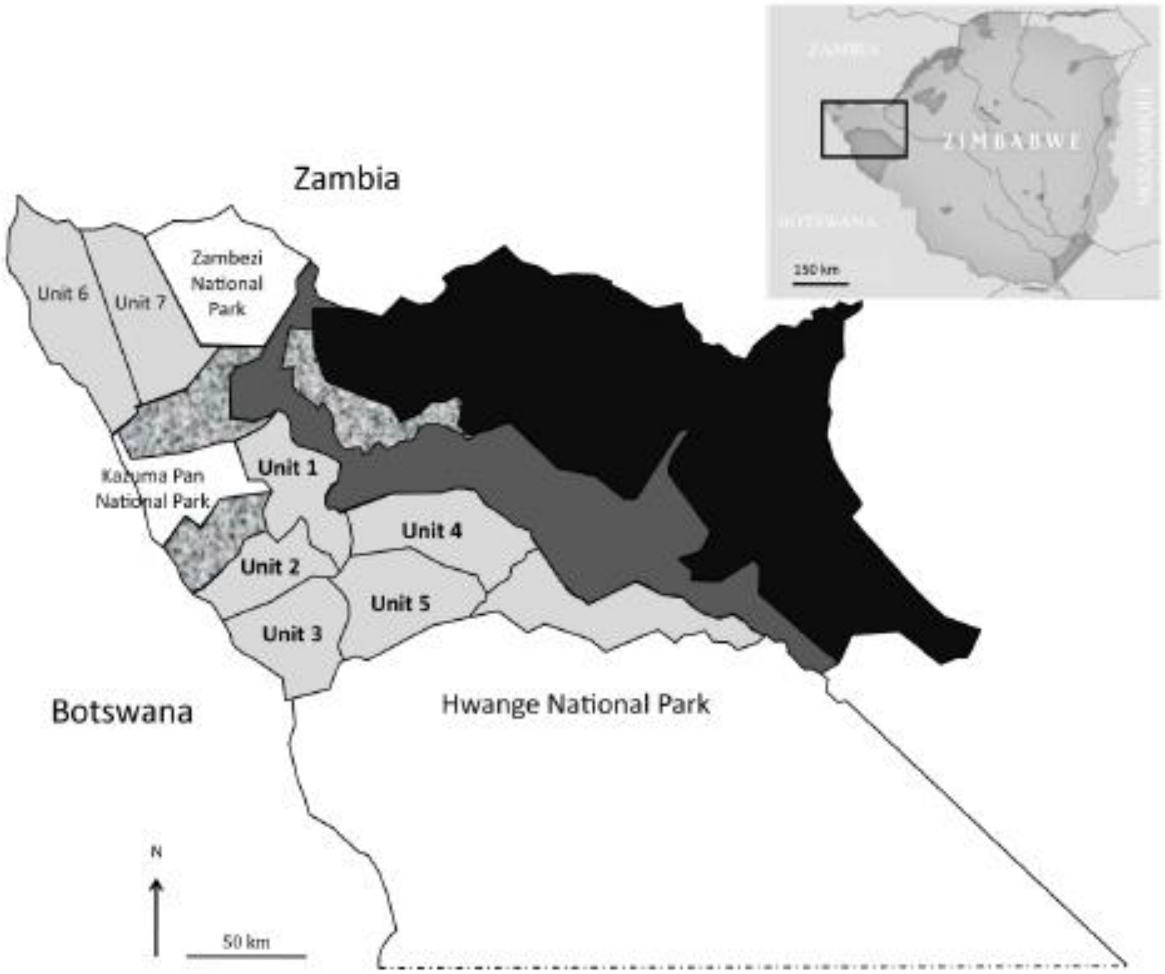


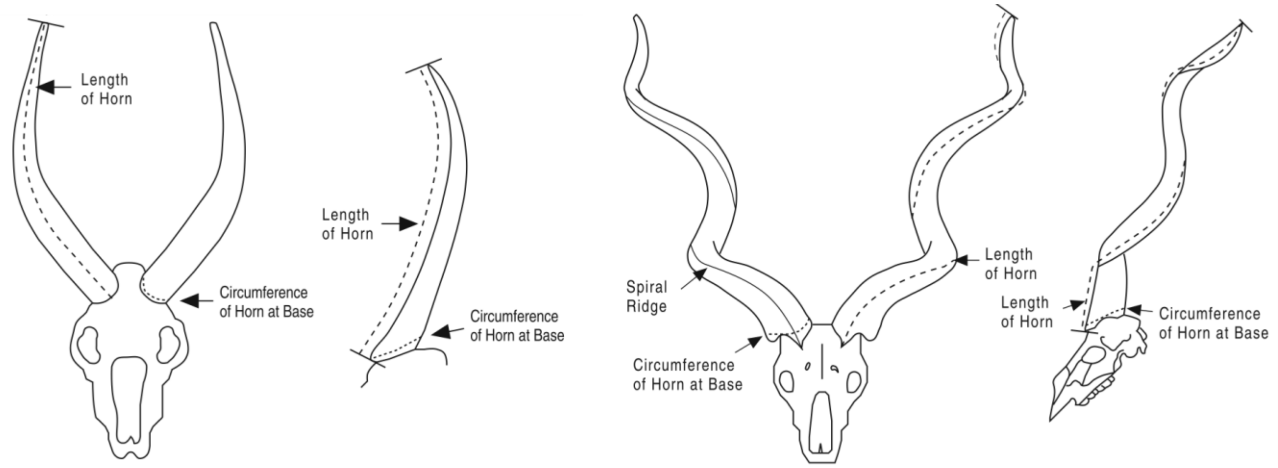
Figure 4.1: Northern part of Hwange ecosystem, Zimbabwe. The study area is delineated by the thick black rectangle. National parks (i.e. hunting-free areas) are coloured in white, hunting areas (units one to seven) of the Matetsi Safari Area in light grey, hunting areas of the Forestry Commission in granite. Private lands and communal lands are respectively coloured in dark grey and in black. The studied hunting areas, units one to five, are indicated in bold font.

Species

We selected three ungulate species for the study, impala *Aepyceros melampus*, greater kudu *Tragelaphus strepsiceros*, and sable antelope *Hippotragus niger* (see Plate 1). Impala and greater kudu are fairly common in Southern Africa, particularly in Zimbabwe (East, 1999). The Hwange ecosystem hosts one of the highest densities of sable antelope in Southern Africa (East, 1999), but sable antelope is rarer than impala and greater kudu (Chamaillé-Jammes, et al., 2009; Peace Parks Foundation, 2009).

Plate 1: (Top) From left to right, adult males of impala, sable antelope, and greater kudu (photo credit: ©Maël Le Corre). (Bottom) Measurement of horn size according to the Safari Club International system (www.scirecordbook.org/docs/methods) for a) simple horned species (i.e. impala, and sable antelope), and b) spiral-horned species (i.e. greater kudu).

a) b)



Sable antelope and greater kudu are more popular trophy species than impala (Lindsey et al., 2006). Sable antelope hunts are more expensive than hunting greater kudu or impala, with safari and trophy fees reaching ca. US$23,000, US$6,500, and US$5,500, respectively (Booth, 2009; Zindele Safaris, 2012). Moreover, sable antelope are generally sold as the flagship species of a safari, whereas greater kudu and impala usually come as add-on components of big game safaris (i.e. lion *Panthera leo*, leopard *Panthera pardus*, elephant *Loxodonta africana*, or buffalo *Syncerus caffer*). Hunters are therefore expected to be more selective when hunting sable antelope compared to impala, and to greater kudu to a lesser extent. Hunts of the three species are essentially for trophy animals (i.e. adult males). However, in impala and greater kudu, females are also hunted on quotas for food rations and baits for hunting carnivores. For impala, 33±23% (min = 0, max = 100) of harvested animals in MSA from 1977 to 2008 were females, and 21.4±16.4% (min = 0, max = 82) for greater kudu. For sable antelope, less than 15±15% (min = 0, max = 55) of harvested animals were females between 1973 and 1981, and none since 1981 (ZPWMA, Unpublished data).

Hunting organization and trophy data

The hunting season runs from March to December (although there is no ‘closed’ season). Professionally qualified hunting guides, and ZPWMA’s rangers accompany trophy hunters during their safari to assist selection of trophy animals and monitor hunts. Trophy fees do not increase with trophy size, so that hunters preferentially target the largest-horned males without any financial limitation. Compulsory measurement and aging of harvested animals by ZPWMA’s staff takes place at the MSA headquarters. ZPWMA financially penalises safari operators for harvest animals younger than two years old. Therefore, whereas there is no lower limit on trophy size, harvested males are almost exclusively adult males.

ZPWMA allocates hunting quotas on the basis of aerial censuses, ground reconnaissance by rangers and reports from professional hunters. Detailed information on population size, structure, and dynamics is usually lacking in hunting areas, so that excessive harvesting levels may occur and result in decline of population size and trophy quality. In MSA, however, information on ungulate populations is available, quotas are adjusted annually, and have historically been assumed to be conservative (Booth and Jones, Unpublished report).

Horn length was measured on harvested males with a soft tape to the nearest 0.5cm (see Plate 1). For consistency, we systematically used the values for the left horn of each trophy.

The locations where animals were harvested were recorded to the nearest km on printed maps of the hunting units. We extracted these locations with ArcView 3.2 (ESRI, Redlands, California, USA). Age was determined following the teeth attrition method (Spinage, 1971). Teeth wear of harvested animals was compared against a series of mounted specimens of known age. This aging method appears to be robust to differences in habitat, climate and management (for red deer *Cervus elaphus*; Lowe, 1967), and has been validated by the cementum line counts method developed and used for temperate zone animals (Spinage, 1973).

All data were collated by ZPWMA’s officers on printed datasheets, and filed in folders at MSA Headquarters since 1974. While the database is largely complete, some datasheets have been lost and some variables were not consistently recorded over the 30 year period. We also only recorded every second year of impala data because of time constraints. Consequently there are some gaps in the data available for analysis (Table 4.1).

Population data

Road counts were carried out each year late in the dry season (September ⁄ October) in all units and using most available roads as transects following the Distance Sampling procedure (Buckland et al., 2001; Chamaillé-Jammes et al., 2009 for a similar procedure in the neighbouring HNP). We analyzed data using Distance Sampling software (Thomas et al., 2006), and obtained estimates of population size/densities for most ungulate species, per year, and per hunting unit. For each group encountered, group size, sex and age class (i.e. adult, yearling, juvenile) of individuals were recorded. We could therefore estimate the number of adult males of each species in each hunting unit. We then computed the trophy hunting pressure (i.e. number of adult males harvested / number of adult males estimated in the population) for each year and each unit (further information on hunting pressure and densities are in Appendix 4.1). Mean trophy hunting pressure throughout the study period was 0.10±0.09. However, it differed among the three studied species ($F_{2,\ 294} = 21.1$, $P < 0.0001$), with higher averaged trophy hunting pressure for sable antelope than for impala (IC95%=[0.04; 0.10]; $P < 0.0001$) and to a lower extent for greater kudu ([0.02; 0.07]; $P < 0.001$), whereas no difference was observed between greater kudu and impala ([-0.01; 0.05], $P = 0.2$) (see Appendix 4.1a for trends in trophy hunting pressure).

Table 4.1: Sample size (n) and period for which data were available for each trophy variable (i.e. horn length, age, and location of harvested males) for impala, greater kudu, and sable antelope, in hunting units one to five of Matetsi Safari Area, Zimbabwe.

Variables		impala	greater kudu	sable antelope
Horn length	n	1,435	1,163	1,560
	period	*1974-2008*	*1976-2008*	*1974-2008*
Horn length et *Age*	n	609	158*	614
	period	*1986-2006*	*1991-1994,* *2007-2008*	*1982-2008*
Mean age	n		31**	
	period		*1974-2008*	
Horn length et Location	*n*		955	
	period		*1979-2008*	
Horn length, Age et Location	n	457		600
	period	*1986-2002*		*1982-2005*

* 158 animals for which we had both horn measurements and age estimate.
** From a summary table provided by ZPWMA, where mean ages (and standard deviations) from 1057 trophy animals were computed for each year over the period 1974-2008. We used this table to explore temporal trends in mean age of greater kudu.

Foraging competition may be exerted by conspecifics, and by species of the same guild (for impala: buffalo, elephant, greater kudu, warthog *Phacochoerus africanus*, plains zebra *Equus burchelli*; for greater kudu: common duiker *Sylvicapra grimmia*, elephant, impala; for sable antelope: buffalo, elephant, reedbuck *Redunca arundinum*, waterbuck *Kobus ellipsiprymnus*, plains zebra) (Bothma et al., 2002). We calculated the total metabolic biomass of competitors for each species, per year and unit, using referenced metabolic body mass (Cumming et Cumming, 2003) and population estimates from road counts. For harvested males of known age, we computed competition indices, i.e. the average densities of conspecifics (i.e. intraspecific competition, referred as ‘density’ effect), and the average metabolic biomass of potential competitors (i.e. intra and extra-specific competition referred as ‘competitors’ effect) during the years when most horn growth was achieved.

The expected effect of competition should be greater during this period, i.e. the first two years for impala, and four years for greater kudu and sable antelope as determined below.

Environmental variables

For harvested males with a location recorded, we calculated the distance to the closest national park (i.e. "distance NP" effect) with the nearest features extension in ArcView 3.2 (Jeness, 2007). Around each harvest location, we drew a circle of radius 4km for sable antelope and 3km for impala and greater kudu with the Xtools extension (DeLaune, 2003). We chose slightly larger circles than the average home ranges of species in this region (ca. 25km^2, 8.5-13km^2, and 4-10km^2, for sable, greater kudu and impala, respectively; Estes, 1991) to account for the ca. 1km uncertainty in reported location. We assumed that it was a good representation of the home ranges of males well because these species are sedentary and constrained in their movements by the location of water sources (Estes, 1991; Redfern et al., 2003). We used the satellite-derived normalized difference vegetation index (NDVI) as a proxy of vegetation productivity in the drawn circles (i.e. 'productivity' effect) (Ganzin et al., 2005). We used 10-day NDVI images (resolution 1.2 x 1.2 km) derived from 1986 to 2008 from Advanced Very High Resolution Radiometer/National Oceanographic and Atmospheric Agency satellites. The Institute for Soil, Climate, and Water, from the South African National Agricultural Research Council, provided NDVI images. We summed the 10-day NDVI images from October to May (included), corresponding to the rainy season (i.e. vegetation growing season), for each year. NDVI values observed in the home range of harvested males during the years when most horn growth was achieved were then averaged.

Statistical analyses

Because horn length is usually positively related to age (e.g. Côté et al., 1998; Festa-Bianchet, 2004), we first investigated patterns of horn growth by using regressions (linear and non-linear) of horn length against age of harvested males. We then used regressions between age of harvested males and year to test whether trophy hunting skewed the male fraction of the harvested populations towards younger age classes. For the analyses of temporal trends in horn length, it was essential to control for age of harvested males to determine whether possible trends in horn length originated from the alteration of male age structure or another factor. Because this was only feasible for a restricted period of our dataset (Table 4.1), we performed the analyses in two steps: 1) we first carried out regressions of horn length on years over the entire study period to document the general temporal trend of trophy size from the mid-1970s, i.e. when trophy hunting began in MSA, to 2008 for each of the three species; 2) we then corrected for age in the analyses (for the years with age data available, Table 4.1) by using the residuals of the regression between horn length and age, and regressing them in linear models against year as the main variable, and density of conspecifics, biomass of competitors, habitat productivity, and distance to the nearest national park as co-variables. We also tested the effect of the interaction between years and distance to national parks because we expected that the possible decline of horn length would be more pronounced further away from hunting-free areas. However, for greater kudu, since trophy animals were only aged in 1991-1994 and in 2007-2008, we could not correct for age in the analyses. We thus carried out analyses on horn length directly, but could not discount that any trend observed in horn size could be due to a trend in mean age of harvested males.

For the selection of models, we used the backward step-wise selection procedure with successive removals of variables for which $P > 0.05$ (Sokal et Rohlf, 1995). Statistical analyses were performed with R software (http://cran.r-project.org).

Results

Horn growth patterns

Horn length increased with age quadratically in impala (age, $F_{1, 606} = 4.2$, $P = 0.04$; age^2, $F_{1, 606} = 23.7$, $P = 0.001$) and greater kudu (age, $F_{1, 155} = 1.4$, $P = 0.2$; age^2, $F_{1, 155} = 5.2$, $P = 0.02$), whereas it increased linearly in sable antelope ($F_{1, 612} = 16.1$, $P = 0.0001$). In impala, age of harvested males ranged from one to ten years old. At one year of age, horns were 43±7cm long, and then oscillated around 50cm in subsequent age classes (mean±sd = 50.3±3.5cm; Fig. 4.2a). Most horn growth thus occurred during the first two years of life. In sable antelope and greater kudu, age of harvested males ranged from four to ten years, limiting our understanding of on how horn growth was distributed over the first years of

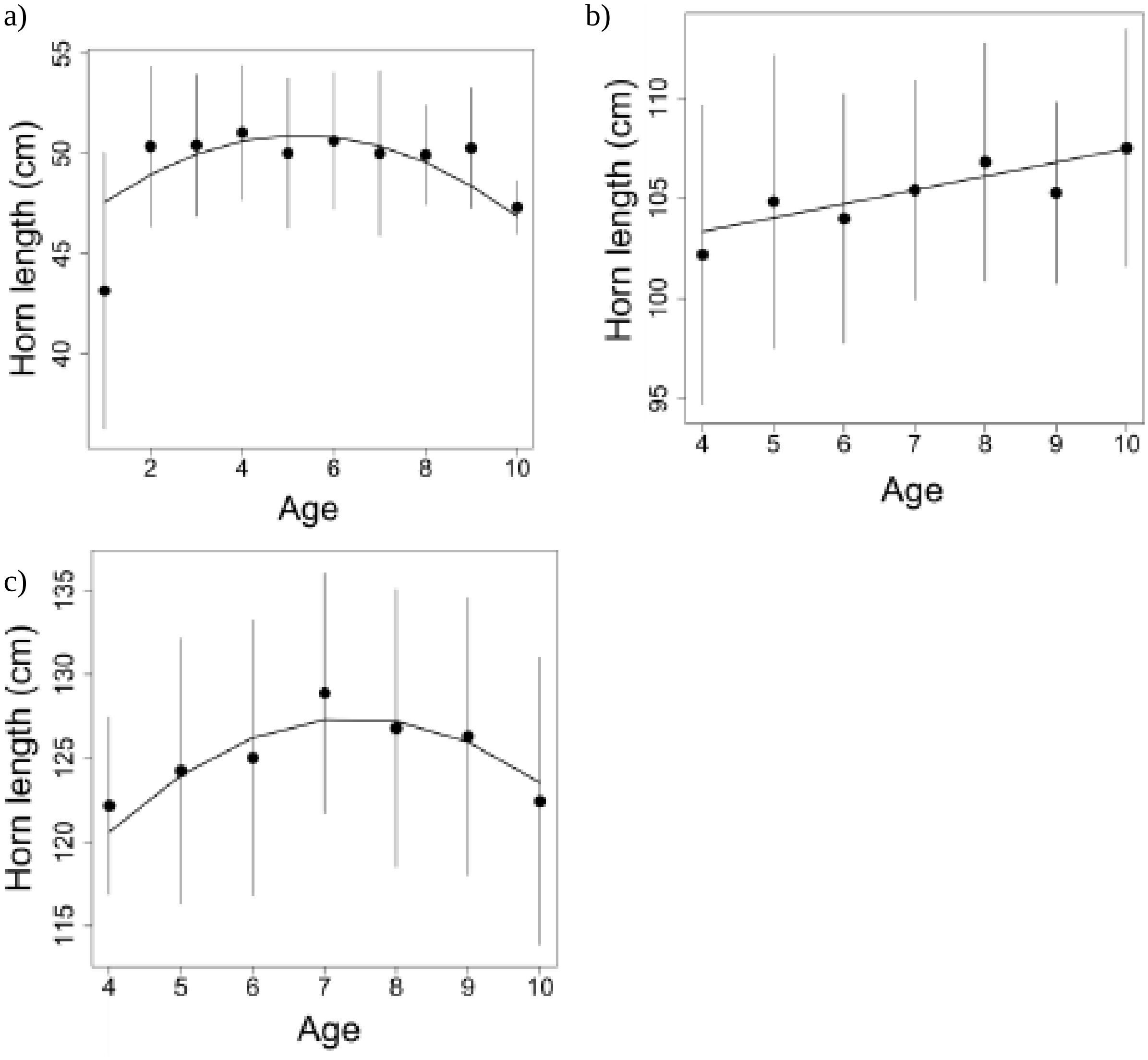


Figure 4.2: Horn length as a function of the age of harvested males in hunting units one to five of Matetsi Safari Area, in Zimbabwe, for a) impala, b) sable antelope, c) greater kudu. Lines are used for significant trends. Dots represent the average horn length of trophy animals per age, and bars the standard deviations.

life. At four years old, horns were already 102±7cm long in sable antelope (Fig. 4.2b), and 122±5cm long in greater kudu (Fig. 4.2c). Horns do not grow over ca. 110cm in sable antelope, and stabilize between ca. 120 and 130cm in greater kudu. Most horn growth thus occurs before four years of age in these two species. We thus predicted that the potential effects of density of conspecifics, biomass of competitors, and vegetation productivity on horn length should occur during the years when most horn growth is achieved, i.e. the first two years for impala, and the first four years for sable antelope and greater kudu.

Temporal trend in age of harvested males

Because age is a major determinant of horn length, we first explored the possibility of a change in age of hunted males during the study period. Trophy age decreased with year in impala ($F_{1,\,607}$ = 20.1, $P < 0.0001$) (Fig. 4.3a), increased quadratically in greater kudu (year, $F_{1,\,28}$ = 6.7, P = 0.02; year^2, $F_{1,\,28}$ = 9.6, P = 0.004) (Fig. 4.3c), whereas we observed no change for sable antelope ($F_{1,\,612}$ = 1.1, P = 0.3) (Fig. 4.3b).

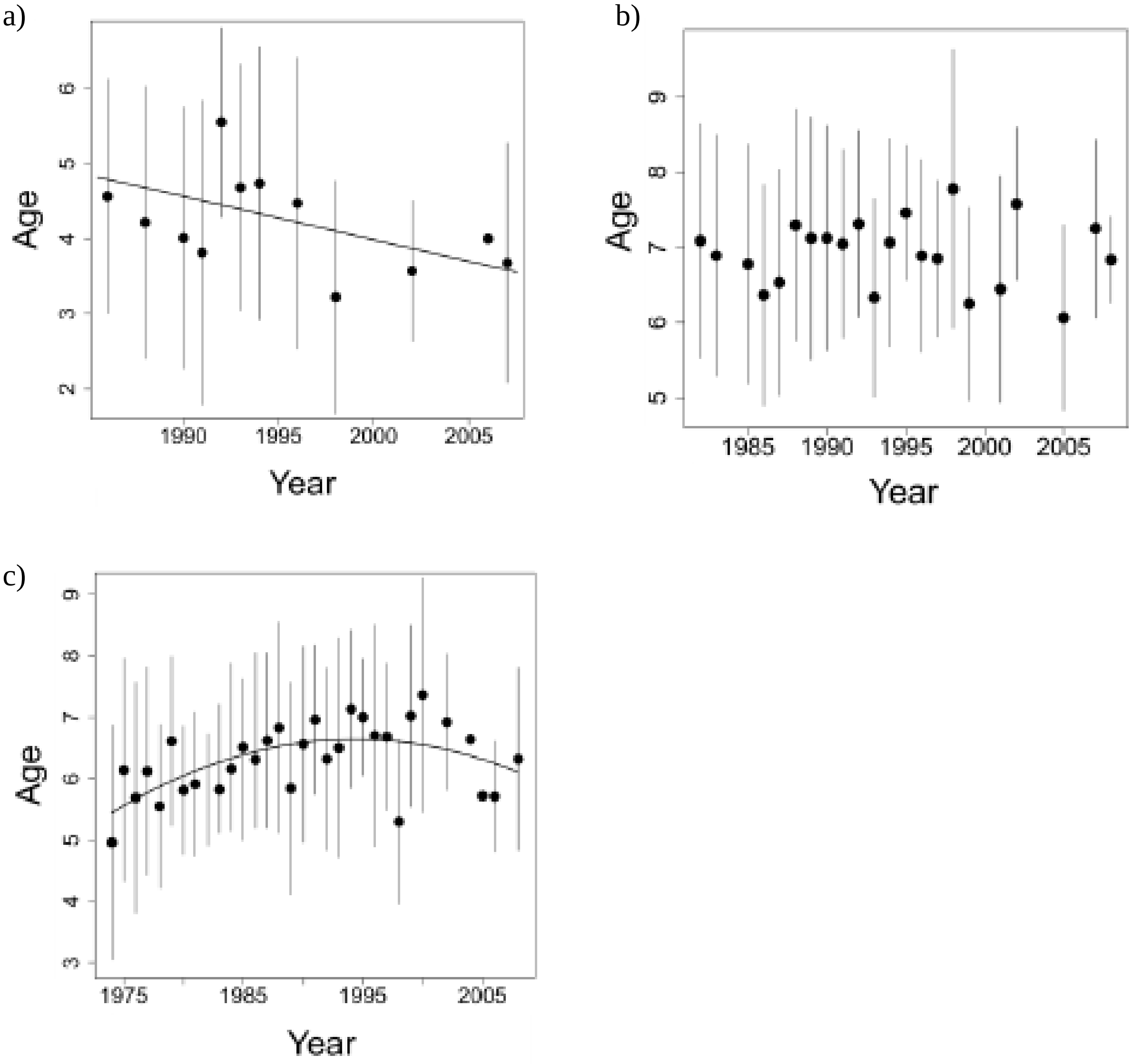


Figure 4.3: Temporal trend of age of harvested males in hunting units one to five of Matetsi Safari Area, Zimbabwe, for a) impala, b) sable antelope, c) greater kudu. Lines are used for significant trends. Dots represent the average age of trophy animals per year, and bars the standard deviations.

Changes in horn length with year and other co-variables

From 1974 to 2008, in general, horn length decreased in impala ($F_{1, 1433} = 46.1$, $P < 0.0001$; Fig. 4.4a) with a loss of ca. 2cm (i.e. 4%), and in sable antelope ($F_{1, 1558} = 135.3$, $P < 0.0001$; Fig. 4.4b) with a loss of ca. 6cm (i.e. 6%). In greater kudu, however, horn length increased quadratically (year, $F_{1, 1160} = 109.4$, $P < 0.0001$; year^2, $F_{1, 1160} = 60.9$, $P < 0.0001$), with a sharp increase of ca. 15cm (i.e. 14%) from 1976 to the mid-1980s, and stable horn length thereafter (Fig. 4.4c).

In the full model, i.e. after correction for age of harvested males, and including the co-variables "Year, Density, Competitors, Distance NP, and Productivity", horn length in impala still decreased, but only between 1986 and 1994. After 1994, horn length increased so that we failed to detect any general trend between 1986 and 2002 (Table 4.2, Fig. 4.5a). In sable antelope, we observed a general decrease in horn length, which accelerated from 1987 onwards (Table 4.2, Fig. 4.5b). In greater kudu, once we included the co-variables, we still observed a sharp increase of horn length between 1979 and the mid-1980s, and stable horn length thereafter (Table 4.2, Fig. 4.5c). Two distinctly contrasting periods were apparent, pre-1985 (mean horn length ± sd = 114.9 ± 8.3cm) and post-1985 (mean horn length ± sd = 125.4 ± 8.6cm) (Wilcoxon signed rank test: $W = 26499.5$, $P < 0.0001$). During each period, we observed no change of horn length over time (pre-1985, $F_{1, 199} = 0.8$, $P = 0.4$; post-1985, $F_{1, 693} = 0.2$, $P = 0.7$).

Horn length decreased with distance to national parks in impala, whereas it increased in sable antelope, and tended to increase in greater kudu, with no significant interaction with year for any of the three species (Table 4.2). In sable antelope and greater kudu, horn length increased quadratically with density, whereas in impala we observed no effect of density on horn length (Table 4.2). Nor average metabolic biomass of competitors, neither vegetation productivity during years of horn growth significantly affected horn length for the three species (Table 4.2) (see Appendix 4.1b).

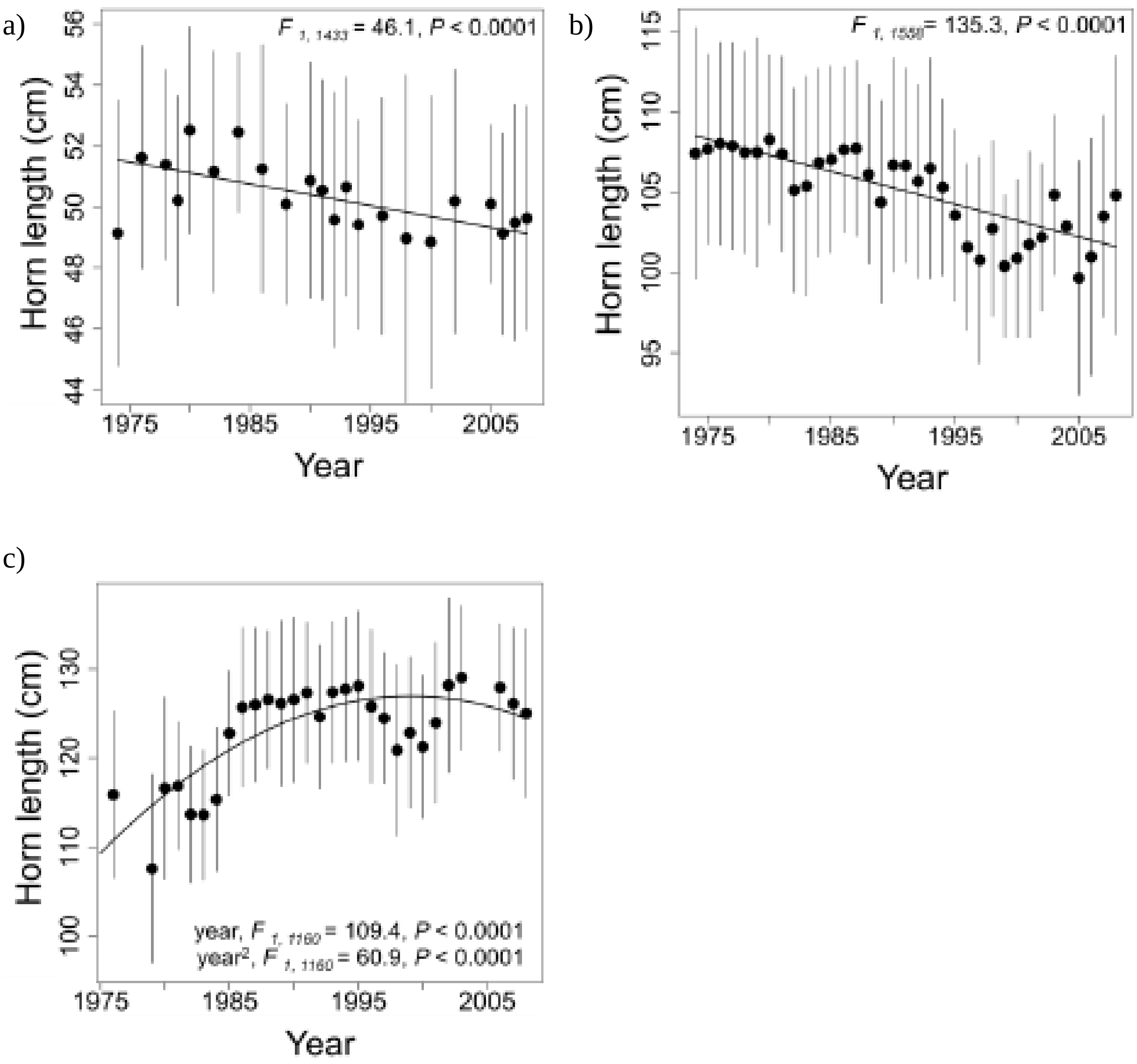


Figure 4.4: Overall temporal trend in horn length of harvested males in hunting units one to five of Matetsi Safari Area, Zimbabwe, for a) impala, b) sable antelope, and c) greater kudu. Lines are used for significant trends. Dots represent the average horn length of trophy animals per year, and bars the standard deviations.

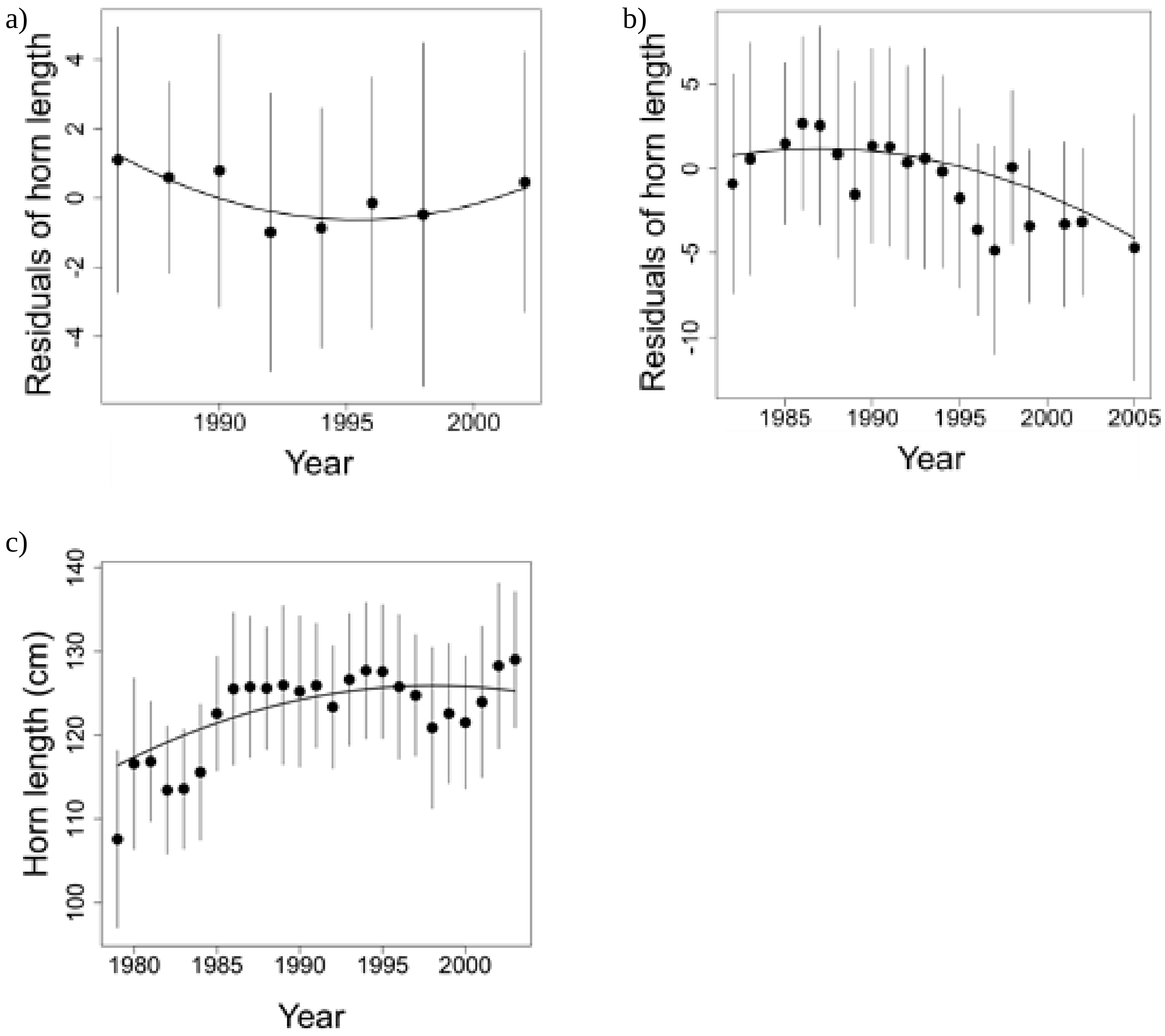


Figure 4.5: Temporal trends in horn length of harvested males once accounting for age and covariates in hunting units one to five of Matetsi Safari Area, Zimbabwe for a) impala, b) sable antelope, and c) greater kudu. Lines are used for significant trends. Dots represent the average horn length of trophy animals per year, and bars the standard deviations.

Table 4.2: Results of the different models on the residuals of horn length for impala and sable antelope, and horn length for greater kudu in Matetsi Safari Area, Zimbabwe.

	Species		
Variables	impala	greater kudu	sable antelope
Year	*$(F_{1,453} = 1.91, P = 0.17)$*	105.30±29.03 $F_{1,949} = 109.92$, $P < 0.0001$	0.65±0.23 $F_{1,594} = 43.41$, $P < 0.0001$
$Year^2$	0.02±0.007 $F_{1,453} =11.31$, $P = 0.0008$	– 0.03±0.01 $F_{1,949} = 53.63$, $P < 0.0001$	– 0.02±0.01 $F_{1,594} = 7.48$, $P = 0.006$
Density	*$(F_{1,451} = 0.21, P = 0.64)$*	4.51±1.26 $F_{1,949} = 40.19$, $P < 0.0001$	3.19±0.87 $F_{1,594} = 17.81$, $P < 0.0001$
$Density^2$	*$(F_{1,450} = 0.60, P = 0.44)$*	– 0.44±0.21 $F_{1,949} = 4.02$, $P = 0.04$	– 0.54±0.23 $F_{1,594} = 5.69$, $P = 0.02$
Distance to National Parks	– 0.03±0.001 $F_{1,453} = 5.37$, $P = 0.02$	*$(F_{1,949} = 3.81, P = 0.051)$*	0.03±0.02 $F_{1,594} = 11.48$, $P = 0.0007$
*Year * Distance to National Parks*	*$(F_{1,452} = 0.73, P = 0.39)$*	*$(F_{1,948} = 0.57, P = 0.45)$*	*$(F_{1,593} = 0.01, P = 0.91)$*
Competitors	*$(F_{1,426} = 0.26, P = 0.61)$*	*$(F_{1,104} = 3.02, P = 0.09)$*	*$(F_{1,539} = 0.20, P = 0.66)$*
Productivity	*$(F_{1,325} = 0.17, P = 0.68)$*	*$(F_{1,74} = 0.06, P = 0.81)$*	*$(F_{1,99} = 0.12, P = 0.73)$*

Results are presented as slope estimates ± SE, and in italics and between parentheses when $P > 0.05$.

Discussion

Horn growth, trophy size and access to females

Most horn growth is completed before two years of age in impala as previously observed by Spinage (1971), and four in sable antelope and greater kudu. Males of these species do not mate before five or six years of age, i.e. when they are socially dominant enough to monopolize mating opportunities, whereas they are physiologically able to reproduce before (Wilson et Hirst, 1977; Murray, 1982; Owen-Smith, 1993). This indicates that males become potential trophies for hunters before reaching the age and social status allowing them to reproduce. Therefore, the selective effect of trophy hunting in these species is likely to be high.

Changes in horn length over time

From 1974 to 2008, horn length decreased by 4% in impala, and 6% in sable antelope. In impala, age of harvested trophy males also declined over time. Because horn length increases with age (this study; Côté et al., 1998; Festa-Bianchet, 2004), it may be difficult to determine whether a decline in horn length is due to a decrease in age of harvested males, or to possible evolutionary change. Indeed, in impala, once we corrected for age of harvested males, horn length no longer showed a decline with year. This suggests that horn length in impala has declined mostly because trophy males were harvested at increasingly younger ages over time. Trophy hunters preferentially harvest older males because they generally have longer horns than younger males. Between years, this may therefore shift the surviving male segment of hunted populations towards younger age classes, as has previously been observed in several other hunted ungulate populations (e.g. Solberg et al., 1999; Laurian et al., 2000). Conversely, in sable antelope, age of trophy males did not change over time, whereas horn length declined. These data suggest that male sable antelopes, following years of a selective harvesting regime, require a longer time to horns of a given length. Trophy hunting may thus have promoted the reproductive contribution of males with slow-growing [or overall smaller] horns (Garel et al., 2007).

The difference between impala and sable antelope is consistent with our prediction based on hunting pressure and trophy value. Over the study period, sable antelope were subjected to higher hunting pressure than impala. Moreover, because it is the most valuable ungulate species, hunters were more selective when hunting sable antelope compared to impala. Not surprisingly then, the decline of horn size only occurred in sable antelope. Such interspecific comparisons in response to trophy hunting are still rare because studies have focused on single species so far (Coltman et al., 2003; Garel et al., 2007).

For greater kudu, we expected horn length to decline at an intermediate rate compared to those observed in impala and sable antelope since hunting pressure and hunter selectivity were higher for greater kudu than for impala, but lower than for sable antelope. Horn length in greater kudu surprisingly increased by 14% from 1976 to 1985, and remained constant from 1985 to 2008. Because mean age of harvested males also increased in a quadratic way during the study period, the observed increase in horn length could be due to an increasing proportion of older males in the population. Interestingly, during the study period, densities of greater kudu globally increased in all the hunting units whereas hunting quotas did not, with the result that hunting pressure declined in every hunting unit (Appendix 4.1a). Such decreases of hunting pressure could partly explain the increase of horn length in greater kudu, with males having the opportunity to survive to older ages and to grow longer horns. The increase of horn length in greater kudu could alternatively reflect the observation that the industry of trophy hunting only started to become popular in the mid-1980s in the region, and therefore hunters truly began to look for long-horned greater kudu males at this time. The absence of such contrasted periods in horn length trends for impala and sable antelope, however, does not support this hypothesis. It could nonetheless be that the trophy value of impala and sable antelope did not change before and after the mid-1980s, i.e. impala remaining a secondary trophy species, and sable antelope a prized trophy species during the whole study period. Furthermore, it is worth mentioning that greater kudu is a spiral-horned ungulate. Therefore, by considering only horn length in our study, we might have overlooked changes that could have operated on other traits, such as horn shape (e.g. width of curves) (e.g. Garel et al., 2007).

Less pronounced trends than for ungulate horn size in previous studies

Overall, the trends of horn size observed in our study were less pronounced than in the two previous empirical studies of ungulates hunted for trophy, i.e. 30% decline over 30 years for the bighorn sheep *Ovis canadensis* of Ram Mountain (Coltman et al., 2003), and 12% decline over 20 years for the Mediterranean mouflon of Caroux-Espinouse Massif *Ovis gmelini musimon* x *Ovis sp.* (Garel et al., 2007). In these two populations, the yearly proportion of adult males harvested was ca. 40% and 20%, respectively (Coltman et al., 2003; M. Garel personal communication), whereas it was on average 5%, 7.5%, and 12% in our study for impala, grater kudu, and sable antelope, respectively. It seems therefore that hunting pressure in our study area was rather conservative compared to these studies, which could explain the less dramatic trends observed for horn size. In sable antelope, however, hunting pressure occasionally rose to above 20% in some consecutive years (Appendix 4.1a), and was therefore as intense as the hunting pressures observed in Ram Mountain and Caroux-Espinouse Massif. The other major difference is that these sheep populations are small and isolated (Coltman et al., 2003; Garel et al., 2007). Therefore, their gene pool is likely to be small, regionally isolated, and so much more likely to be affected by artificial selection. In comparison, antelope populations of Matetsi Safari Area are relatively large, and also regionally connected with potential gene flow into the area from protected populations over time. Accordingly, trends of horn size for these populations are likely to be less marked, and to take place at a much slower rate than for small and isolated populations.

Effects of resources availability

Availability of forage did not appear to be a factor determining the variations in horn length in our study. First, contrary to previous studies with density-dependent effects on horn growth (Jorgenson et al., 1998; Festa-Bianchet et al., 2004; Schmidt et al., 2007), horn size did not decrease with the density of conspecifics in our study. In impala, density of conspecifics had no effect on horn length, even at the highest densities. In greater kudu and sable antelope, horn length actually increased with density of conspecifics, and eventually stabilized at the highest densities. Inter-specific competition can also be ruled out since we observed no effect of the metabolic biomass of guild competitors on horn length. Contrary to northern ecosystems, African savannas still hold a rich and diverse guild of large predators that, through top-down processes and in conjunction with anthropogenic harvest, may partly limit herbivore populations (Fritz et al., 2011). This may restrict the effects of density dependence and inter-specific competition.

In an alternative argument, density of conspecifics and metabolic biomass of guild competitors could be an index of habitat quality, with highest conspecific densities and biomass of competitors observed in the most productive habitats, where more resources can be allocated to horn growth, and therefore where potentially the largest-horned males could be found. The role of habitat quality, however, should also be ruled out in our study because we found no effect of vegetation productivity on horn length.

Density of conspecifics could rather be viewed as a factor of dilution (Hamilton, 1971; Dehn, 1990), with the risk for a given male to be encountered, and shot by hunters, possibly decreasing as densities of conspecifics increase. Therefore, the likelihood that a male would survive longer and grow longer horns increases with densities of conspecifics. Additionally, we suspect that as densities decrease, the opportunities for hunters to find large trophy males also decrease. Therefore hunter selectivity should decline along with the horn length of harvested individuals.

Effects of distance from hunting-free areas

Horn length decreased with distance from national parks for impala, but not for greater kudu and sable antelope. Inter-specific differences in the effect of distance from national parks on horn length could have been expected because home range size is positively related to body mass in African antelopes (du Toit, 1990). Therefore, males of the smallest species, i.e. impala, should disperse over shorter distances from national parks compared to males of larger species, i.e. greater kudu and sable antelope. We thus expected the decline of horn length with distance from the hunting-free areas to be inversely linked to body size, i.e. a stronger decline in impala –as we observed- compared to greater kudu and sable antelope. For sable antelope, and greater kudu to a lesser extent, longer-horned males were surprisingly found at greater distances from national parks. This counter-intuitive result could be explained by a higher hunting pressure in hunting areas closest to the national parks (Appendix 4.1a). We suspect that because of their proximity to the national parks these hunting areas were believed to be able to sustain higher hunting pressure than areas further away, or alternatively, that trophy hunters preferentially hunt along boundaries of national parks where there is an expectation that higher densities of large males may occur. Higher hunting pressure in the immediate periphery of national parks may therefore act as a barrier to males' dispersal, reducing their dispersion from national parks further into hunting areas. In addition, densities of sable antelope have declined in the region for the past decades, particularly in Hwange National Park where densities are four times lower than in the hunting areas (Crosmary et al., unpublished data). In this case National parks are unlikely to act as a source for the hunting areas.

Biological effects of decline in horn size

When horn length declines primarily because of a decrease of older males in a population, such as in impala in our study, evolutionary processes are not necessarily involved.

Nonetheless, when the proportion of adult males declines in hunted populations, young males usually increase their reproductive effort (Solberg et Sæther, 1994; Mysterud et al., 2003) at the expense of body growth, and therefore may experience a decrease in survival (Jorgenson et al., 1997; Singer et Zeigenfuss, 2002). Eventually, reproduction and recruitment may be jeopardized (Singer et Zeigenfuss, 2002; Holand et al., 2003; Sæther et al., 2003). When horn length of harvested males declines independently of age over time, as in sable antelope, it suggests that trophy hunting has artificially selected for males with slow-growing [or smaller] horns, and so that changes in this trait may be genetically determined. Moreover, since horn size and body weight are generally positively correlated (e.g. Coltman et al., 2003; Garel et al., 2007), short-horned males are often also lighter. In ungulates, survival (Guinness et al., 1978; Gaillard et al., 1998) and reproduction (Festa-Bianchet et al., 1998, 2000; Mainguy et al., 2009) are strongly dependent on body mass. Therefore, a decrease of horn size may indirectly have long-term demographic effects on population dynamics.

Conclusion

Our study is one of the rare empirical examples of long-term trends in horn size of ungulates hunted as trophies, and to date the only one for free-ranging African populations. When hunting quotas are conservative and rigorously managed, as it seems to be the case in Matetsi Safari Area, we conclude that temporal trends in horn size are less dramatic than those observed in heavily hunted populations elsewhere. Trophy hunting may therefore be sustainable and benefit conservation of natural habitats. Nevertheless, species exposed to higher hunting pressure and higher trophy selectivity from hunters are more likely to experience a decrease of horn size. This is because hunter preference for large trophy sizes may drive evolutionary selection for individuals with small sized heritable traits- such as horn size. This is the case for sable antelope in our study. The situation of this species in Matetsi Safari Area is particularly critical because there is evidence that the observed decline in horn size could be genetic, and the neighbouring national parks may not act as a source of individuals for the hunting areas. In this case, it may be difficult to reverse the decline in horn size naturally even if hunting quotas were reduced. This may threaten the genetic integrity and conservation of the species in the region. Finally, decline in trophy size could potentially affect income for the hunting industry if hunters choose to travel to areas where sizes of trophies remain attractive. If this occurs eventually the amounts that can be reallocated to conservation programmes in affected areas may be reduced.

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CHAPITRE 5
AUTANT, VOIRE PLUS, A L'EXTERIEUR QU'A L'INTERIEUR

Thirty years of trophy hunting did not affect population densities of large African herbivores in Zimbabwe

WILLIAM-GEORGES CROSMARY, STEEVE D. CÔTÉ, HERVÉ FRITZ

Résumé

La persistance des grands herbivores dans les zones de chasse aux trophées d'Afrique est encore méconnue parce qu'il y a peu de suivis à long terme hors des parcs nationaux. Nous avons comparé les tendances populationnelles de plusieurs espèces de grands herbivores lors des 30 dernières années entre le Parc National de Hwange, Zimbabwe, et l'Aire de Safari de Matetsi adjacente au parc où le prélèvement était de ca. 2% par an. Nous avons examiné si la chasse aux trophées altérait les densités et la proportion de mâles adultes des populations chassées. D'une manière générale, les densités de population étaient autant élevées, sinon plus, dans les zones de chasse que dans le parc national, sauf pour l'éléphant et l'impala. La proportion de mâles adultes ne différait pas entre les deux zones, sauf pour les espèces les plus chassées et avec une plus grande proportion de mâles prélevés. Les densités ont globalement décliné depuis 30 ans dans les deux zones, surtout pour les paisseurs sélectifs, probablement en raison de leur plus grande sensibilité aux variations de précipitations que les autres herbivores. Les précipitations ont en effet diminué au cours de la période d'étude, et les sécheresses ont été particulièrement sévères et fréquentes durant les années 1990. Les brouteurs, les herbivores au régime alimentaire mixte, et les paisseurs non sélectifs ont globalement moins décliné dans les zones de chasse que dans le parc national. Des densités moindres en prédateurs naturels et en éléphants à l'extérieur du parc national ont peut-être conduit à ce résultat surprenant. Ceci reste cependant à être démontré. Cette étude montre que les grands herbivores africains peuvent persister à long terme dans les zones de chasse aux trophées. Lorsque rigoureusement gérées, ces dernières peuvent être des zones de conservation pertinentes, surtout dans le contexte actuel de déclin généralisé de la faune en Afrique.

Abstract

The persistence of large African herbivores in trophy hunting areas is still unclear because of a lack of data from long-term wildlife monitoring outside national parks. We compared population trends over the last 30 years in Hwange National Park, Zimbabwe, and the neighbouring Matetsi Safari Area where large herbivores were harvested at an average rate of ca. 2% per year. We investigated whether trophy hunting altered densities, and proportion of adult males in several large herbivore populations. Large herbivores generally persisted as well, or even better, in the hunting areas than in the national park. Proportion of adult males generally did not differ between the two zones, except for species with higher harvest rates and proportionally more males harvested. Densities were not lower in the hunting areas than in the national park, except for elephant and impala. Large herbivores generally declined throughout the 30-year period in both zones, but more particularly for selective grazers. This is likely due to their greater sensitivity to variation in rainfall compared to other herbivores. Rainfall indeed declined during the study period, and droughts were particularly frequent during the 1990s. Browsers, mixed-feeders, and non-selective grazers generally declined less in the hunting areas than in the national park, possibly because of lower densities of natural predators and elephants outside the park. However, this hypothesis remains to be investigated. Overall, our study highlighted that large herbivores may thrive in trophy hunting areas as well as in national parks. Trophy hunting areas, when rigorously managed, may be relevant conservation areas, more particularly given the current global decline of wildlife abundance across Africa.

Key words: trophy hunting, large herbivores, Zimbabwe, conservation, protected areas.

Introduction

Hunting increases mortality in harvested populations, and may therefore alter their dynamics (Caughley, 1977). With inappropriate control, hunting may jeopardize the viability of harvested populations, and may eventually drive them to extinction (e.g. poaching: Milner-Gulland et al., 2003a; high hunting quotas: Besnard et al., 2010). Overhunting threatens more than 30% of endangered mammal species (Baillie et al., 2004), particularly in ungulates (Price et Gittleman, 2007). Ungulates often drive the structure, composition, and functioning of ecosystems (Collins et al., 1998; Côté et al. 2004). They moreover provide goods and income to human communities (Milner-Gulland et al., 2003a). Understanding and managing the effects of hunting on ungulate population dynamics is therefore crucial for the integrity of terrestrial ecosystems, as well as for economic interests (Gordon et al., 2004).

Trophy hunting is a legalized hunting mode used worldwide as a conservation option (Dickson et al., 2009). Trophy hunters are willing to pay large amounts of money to harvest individuals with large secondary sexual characters, i.e. horns or antlers (Festa-Bianchet, 2003). This creates incentives for the conservation of natural habitats and animal populations (Leader-Williams et al., 2001). Horns and antlers are particularly developed in males (Johnstone, 1974; Cumming, 1989), and increase as males grow older (Côté et al., 1998; Coltman et al., 2003). Consequently, harvest of trophy hunting is skewed towards adult males, and their proportion may therefore decrease in hunted populations (Laurian et al., 2000). Despite productivity usually considered to be higher in populations with female-biased sex ratio (Caughley, 1977), it is increasingly acknowledged that lack of adult males may alter reproduction, recruitment rates, and eventually population dynamics (reviewed in Milner et al., 2007).

Off-takes in trophy hunting supposedly represent only a small fraction of hunted populations (Cumming, 1989; Caro et al., 1998). In Africa, however, long-term monitoring is rare outside national parks (but see Stoner et al., 2007; Western et al., 2009). Consequently, hunting quotas are often set on inappropriate estimates based on historical or anecdotal observations, and are therefore often unsustainable (e.g. Elkan, 1994; Grobbelaar et Masulani, 2003). Furthermore, law enforcement that should insure quotas are complied and limit overhunting, is financially challenging, and thus often neglected in developing countries (Price et Gittleman, 2007).

These potential effects of trophy hunting on large herbivore populations have fuelled the long-standing debate as to whether trophy hunting may be an effective conservation option in Africa (e.g. Taylor et Dunstone, 1996), especially because there are almost no long-term population surveys in trophy hunting areas (but see Caro et al., 1998). In this context, we compared densities and proportion of adult males of several large African herbivores, between the Matetsi Safari Area (hunting area) and the neighbouring Hwange National Park (hunting-free area), Zimbabwe, over the past 30-years. We tested whether populations of hunting areas had (1) lower densities, (2) lower proportion of adult males compared to populations of the national park. We also tested whether (3) densities and proportion of adult males decreased in hunting areas throughout the past three decades but not, or less, in the national park. We also explored alternative determinant factors of the spatial patterns and temporal trends of large herbivore densities in our study area, i.e. rainfall, and densities of natural predators and elephants.

Methods

Study area

The study covered parts of Matetsi Safari Area (MSA) and Hwange National Park (HNP). MSA is a major hunting complex in Zimbabwe (ca. 3,000 km^2; Cumming, 1989), at the northwestern border of HNP (ca. 15,000 km^2) (Fig. 5.1). MSA and HNP are state-owned lands administrated by Zimbabwe Parks and Wildlife Management Authority (ZPWMA). MSA, however, has been leased to safari operators for hunting tourism since 1973. Seven hunting units constitute MSA, units one to five in the southern part, units six and seven in the northern part. Hunting ceased in unit seven in 1995. Moreover, vegetation types and environmental conditions (i.e. rainfall, temperature, soil characteristics) in units 6 and 7 differ from the five other units (Ganzin et al., 2008; Peace Parks Foundation, 2009). We thus focused on units one to five (404 km^2, 292 km^2, 356 km^2, 470 km^2, and 370 km^2, respectively; Fig. 5.1). In HNP, we covered the blocks that were adjacent to these five

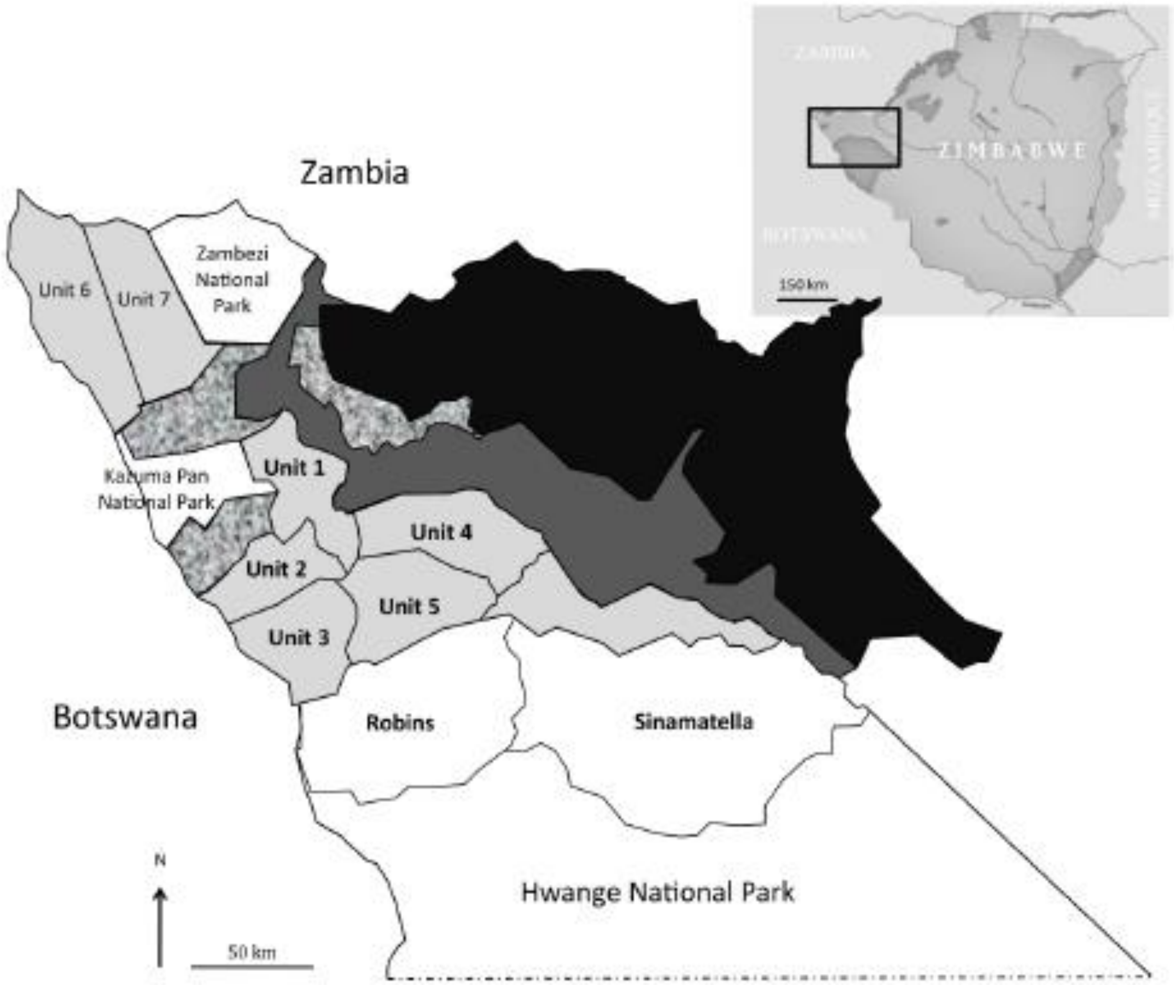


Figure 5.1: Northern part of Hwange ecosystem, Zimbabwe. The study area is delineated by the thick black rectangle. National parks (i.e. hunting-free areas) are in white, hunting areas (units one to seven) of the Matetsi Safari Area in light grey, hunting areas of the Forestry Commission in granite. Private lands and communal lands are respectively coloured in dark grey and in black. The studied hunting units of Matetsi Safari Area and blocks of Hwange National Park are indicated in bold font.

hunting units, i.e. Robins (ca. 1,000 km^2), and Sinamatella (ca. 1,000 km^2) (Fig. 5.1), because they presented similar vegetation types and environmental conditions (i.e. rainfall, temperature, soil characteristics) as MSA (Ganzin et al., 2008; Peace Parks Foundation, 2009). Communal and private lands border the eastern part of the complex, and the western part of units three and two. Unit one is bordered by Kazuma Pan National Park (KPNP, ca. 310 km^2) and by two hunting areas managed by the Forestry Commission (i.e. Kazuma and Panda-Masuie Forests) at the western and northern limits (Fig. 5.1). The study area is located on well-drained shallow rocky soils, where vegetation is typical of southern African dystrophic wooded and bushed savannas, with patches of grasslands, and dominance of *Colophospermum mopane* and *Combretum spp.* (Rogers, 1993; Ganzin et al., 2008). Surface water is mainly found in natural and artificially filled waterholes, and in some rare rivers. During the dry season, natural waterholes and rivers dry up and most of the surface water available to animals is found in artificially filled waterholes and river pools. As state-owned lands, MSA and HNP are similarly managed regarding anti-poaching, surface-water provision, and controlled fires (ZPWMA, Unpublished data).

Species

We studied African buffalo *Syncerus caffer*, Burchell's zebra *Equus burchelli*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, greater kudu *Tragelaphus strepsiceros*, impala *Aepyceros melampus*, reedbuck *Redunca arundinum*, sable antelope *Hippotragus niger*, warthog *Phacochoerus aethiopicus*, and waterbuck *Kobus ellipsiprymnus*. These species are among the most common large herbivores encountered in southern Africa (Skinner et Chimimba, 2005), and are hunted for trophy (Lindsey et al., 2007b). They have contrasted diets and body weight, but are all water-dependent (except warthog and giraffe, Table 5.1). This allows comparisons that may provide insights on alternative factors that could have influenced trends of population densities in our study area. For instance, selective grazers are particularly sensitive to a low rainfall regime (Owen-Smith, 2008), so that their densities may be more affected than other species during dry years. In addition, smaller body-size herbivores are more vulnerable to natural predators than larger preys (Sinclair et al., 2003). Their densities may therefore be more influenced by variation in natural predator abundances than larger body-size herbivores.

Population trends

Yearly road counts were carried out in late dry season (September ⁄ October) from 1977 to 2010 in the hunting units of MSA and the blocks of HNP. Data, however, were missing between 1987 and 1994 in HNP. We therefore divided the dataset into two periods, i.e. 1977-1986 and 1995-2010 in both zones. Most available roads were used as transects following the Distance Sampling procedure with two observers, whose effect was accounted for in the analyses (Buckland et al., 2001; Chamaillé-Jammes et al., 2009 for similar procedure in HNP). We analyzed data using Distance Sampling software (Thomas et al., 2006), and obtained estimates of population densities per species, and per year in each unit/block. Coefficient of variation associated with population estimates averaged 17% in warthog, 14% in impala, 34% in reedbuck, 16% in greater kudu, 35% in waterbuck, 25% in sable antelope, 20% in zebra, 44% in buffalo, 26% in giraffe, and 36% in elephant. For each group of herbivores encountered, species, group size, and number of adult males were recorded. We then computed the proportion of adult males as the ratio of the total number of adult males counted over the total number of individuals counted per species, and per year in each unit/block.

Table 5.1: Main large herbivores of Matetsi Safari Area (MSA, hunting areas) and Hwange National Park (HNP, hunting-free area), classified by diet, dependency on surface water, and ranked according to increasing body weight. Adapted from Bothma et al. (2002).

Species	Diet	Surface water dependency	Mean body weight (kg)
Warthog	selective grazer [a]	no	30
Impala	mixed-feeder	yes	41
Reedbuck	selective grazer	yes	55
Greater kudu	browser	yes	136
Waterbuck	selective grazer	yes	205
Sable antelope	selective grazer	yes	210
Zebra	nonselective grazer	yes	216
Buffalo	nonselective grazer	yes	495
Giraffe	browser	no	700
Elephant	mixed-feeder	yes	1725

[a] Warthog is less selective than other selective grazers, and may occasionally browse (Bothma et al., 2004).

Rainfall regime

Fluctuations in the abundance of herbivore populations in African semi-arid savannas are largely driven by rainfall, particularly during the dry season (Mduma et al., 1999; Ogutu et Owen-Smith, 2003). Although most rain falls in the wet season, from November to April, some falls during the dry season. Data on broad scale annual and dry season rainfalls in the study area were available for 1976-2005. Annual and dry season averages were 544 mm (Fig. 5.2a) and 10.2 mm (Fig. 5.2b), respectively. There was, however, a high variability associated with average annual and dry season rainfalls (CV 32% and 142%, respectively). Despite the period 1995-2010 experienced more years below the long-term average than 1977-1986 (i.e. six *versus* three), annual rainfall did not significantly differ between the two periods (average annual rainfall ± SD: 591 ± 170 *versus* 487 ± 198; Mann-Whitney test: $W = 77$, $P = 0.3$) (Fig. 5.2a). However, the 3-year running means of annual rainfall linearly decreased from 1977 to 2010 (Fig. 5.2a; slope of -6.7 ± 1.7, $F_{1,28} = 15$, $P < 0.001$). Dry season rainfall did not significantly differ between the two periods (14 ± 16 *versus* 13 ± 16; Mann-Whitney test: $W = 68$, $P = 0.6$) (Fig. 5.2b). However, the period 1995-2010 followed a dry spell decade, i.e. 1986-1994, with dry season rainfall constantly below the long-term average (Fig. 5.2b). Therefore, if annual or dry season rainfall were of primary influence on herbivore population dynamics, population densities should generally be lower during 1995-2010 than during 1977-1986 for most herbivore species, both in MSA and HNP.

Harvest rates

Cumming (1989) reported that annual harvest rates for large herbivores in MSA were ca. 2%. Data on hunting quotas for the study period were only available for buffalo, elephant, impala, greater kudu, and sable antelope. We were therefore able to compute harvest rates (i.e. number of harvested animals over the estimated population size) only for these species, and found an average of 1.7±1.2% throughout the study period, similar to Cumming (1989). It, however, varied among species ($F_{4,\ 104} = 10.5$, $P < 0.0001$), with sable antelope and elephant experiencing higher average harvest rates than impala, buffalo, and greater kudu (Fig. 5.3a). Trophy hunters essentially harvest large-horned animals, i.e. adult males.

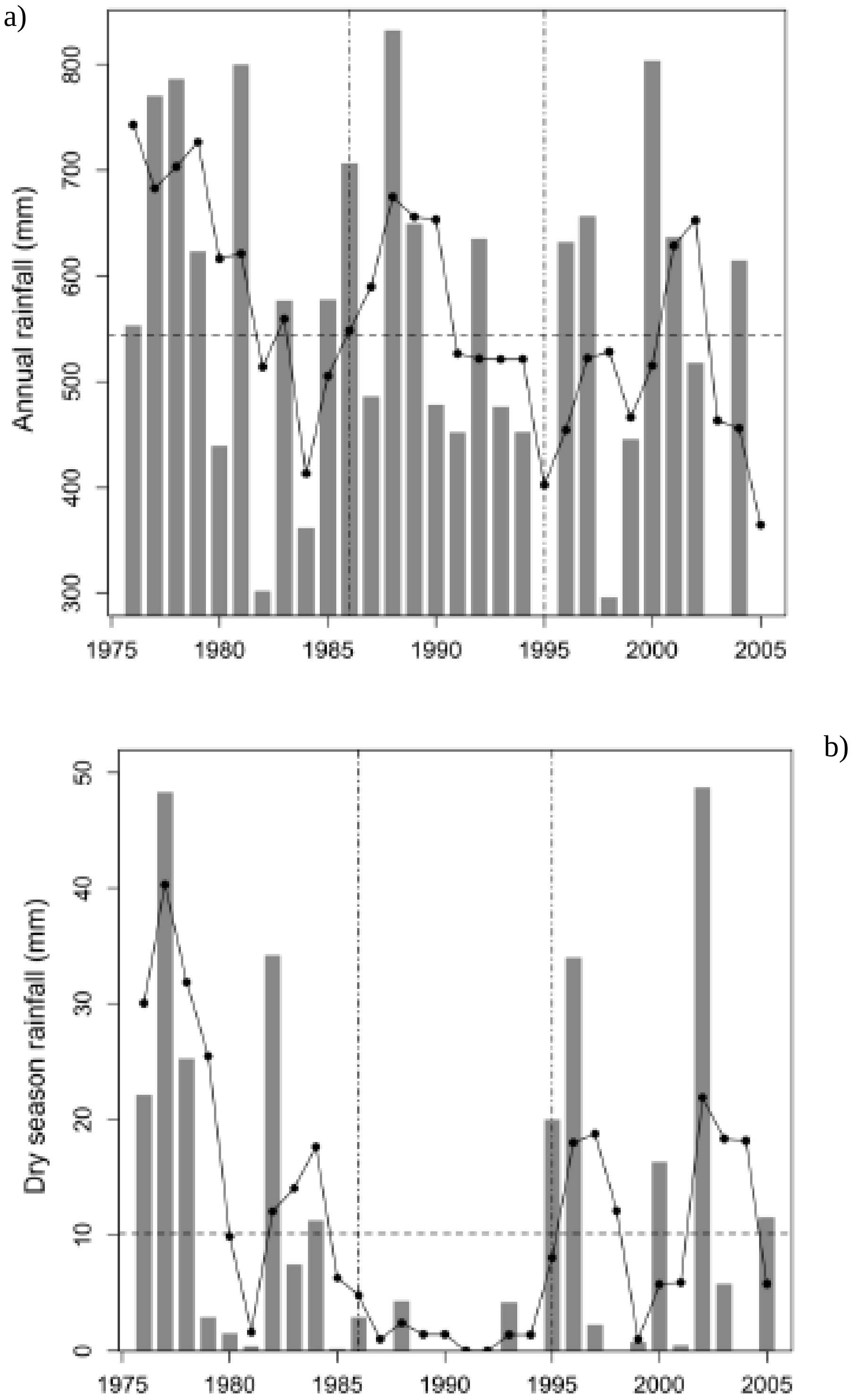


Figure 5.2: Trends in (a) annual rainfall and (b) dry season rainfall over 30 years in units one to five of Matetsi Safari Area (hunting areas), and the blocks of Robins and Sinamatella of Hwange National Park (hunting-free area), Zimbabwe. Bars indicate annual records and solid lines the 3-year running means. The horizontal dotted line represents the long-term average. The vertical dotted lines separate the study periods (see text for details).

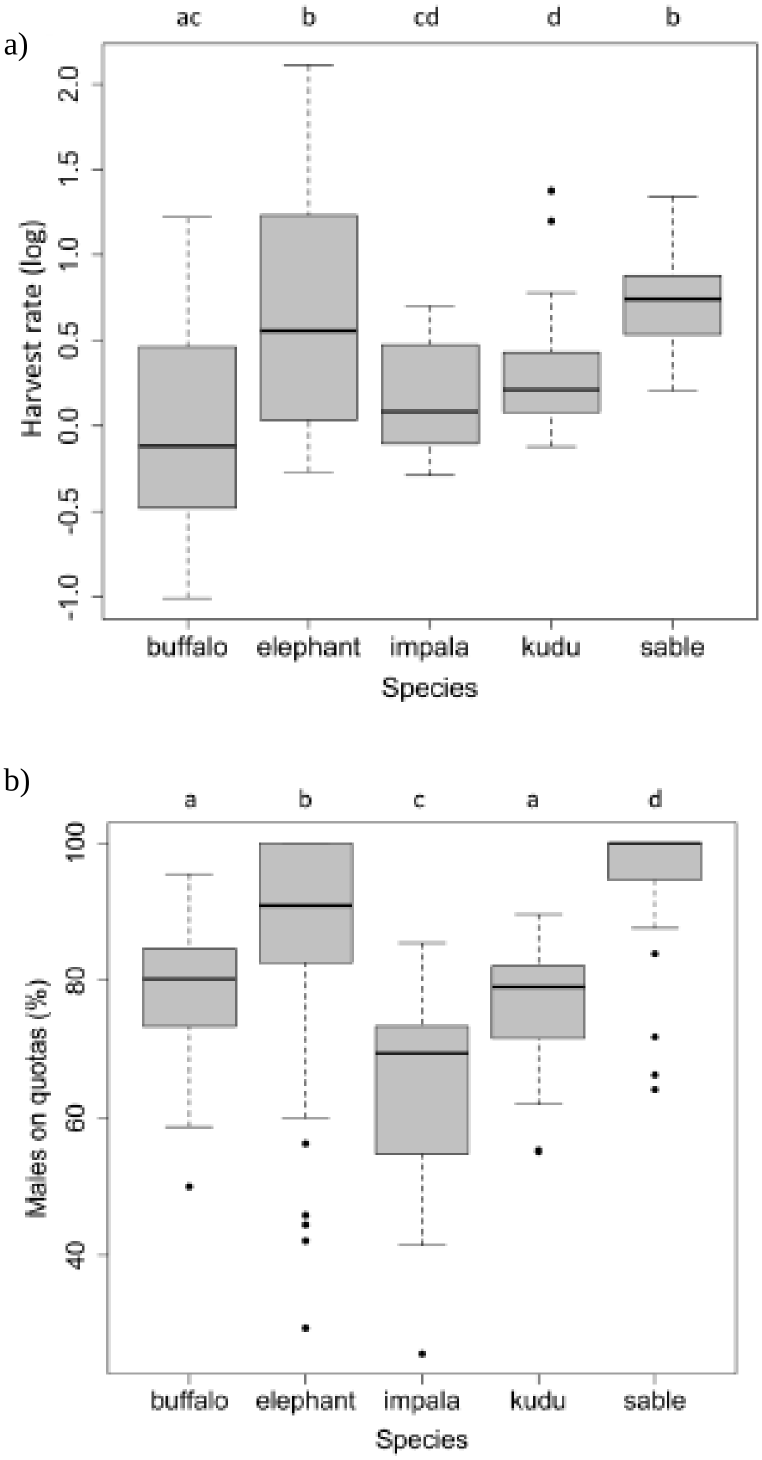


Figure 5.3. Observed values of a) harvest rate, and b) proportion of males in hunting quotas, between 1978 and 2008 in hunting units one to five of Matetsi Safari Area, Zimbabwe, for buffalo, elephant, impala, greater kudu, and sable antelope. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentiles, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are the observation <10th or >90th percentiles. Different letters indicate significant differences at $P < 0.05$.

Females can nonetheless be on quotas for food ration and baits for hunting carnivores. The average proportion of males on quotas was 80±17%, but varied among species ($F_{4,\ 150}$ = 15.7, $P < 0.0001$), being higher for sable antelope and elephant, and lower for impala (Fig. 5.3b). If trophy hunting alters population dynamics and structure, then density and proportion of adult males should be especially low in hunting areas compared to the national park for species like sable antelope and elephant.

Analyses

To test whether population densities and the proportion of adult males differed between hunting areas and the national park, we performed ANOVAs with zone (i.e. MSA versus HNP) and period (i.e. 1977-1986 versus 1995-2010) as factors. We also tested the interaction between zone and period because we expected differences between hunting areas and the national park to increase through time. Because temporal serial autocorrelation may affect time series counts, we controlled for temporal autocorrelation using a first-order autoregressive covariance structure (Pinheiro et Bates, 2000). Densities were square-root transformed, and proportion of adult males were log-transformed to meet normality assumptions. We used units/blocks as random effects in the ANOVAs, using the R nlme package (http://cran.r-project.org).

We then built a tree-based model to test whether there were groups of species whose densities had been similarly affected by zone and period (Breiman et al., 1984). For trends in densities to be compared among species, we first normalized densities for each species before pooling them in a single dataset, with zone, period, and species as factors. We then used the R rpart and partykit packages (http://cran.r-project.org) to build a classification tree of the normalized densities according to these three factors, and then simplified it using the pruning method (Braiman et al., 1984).

Results

Population densities

Throughout the study period, population densities did not differ between MSA and HNP for buffalo, giraffe, greater kudu, reedbuck, warthog, and zebra, whereas they were significantly higher in MSA than in HNP for sable antelope and waterbuck (Table 5.2, Fig. 5.4). Densities were significantly lower in MSA than in HNP for elephant and impala (Table 5.2, Fig. 5.4).

Densities generally declined between 1977-1986 and 1995-2010 in both zones for selective grazers (Table 5.2, Fig. 5.4). In HNP, this decline was ca. 77%, 70%, 33%, and 69% for reedbuck, sable antelope, warthog, and waterbuck, respectively. The decline seemed milder in MSA, i.e. ca. 69%, 56%, 27%, and 51%, respectively for the same species (Fig. 5.4), although the differences were not significant (Table 5.2). Sable antelope densities remained higher in MSA compared to HNP throughout the study period (Table 5.2, Fig. 5.4). Densities of giraffe, impala, and greater kudu, were higher in HNP than in MSA during the period 1977-1986 (Table 5.2, Fig. 5.4). However, they declined between 1977-1986 and 1995-2010 in HNP about 43%, 33%, and 33%, while they increased about 15%, 11%, and 30% in MSA (Table 5.2, Fig. 5.4), so that densities did not differ between zones in 1995-2010. Buffalo tended to experience similar trends than for giraffe, impala, and greater kudu (Fig. 5.4), though not significantly (Table 5.2). For zebra, we observed no temporal trend in densities, and no significant difference between MSA and HNP (Table 5.2, Fig. 5.4). In elephant, densities were generally ca. 98% higher during 1995-2010 compared to 1977-1986. Densities were higher and seemed to increase more in HNP compared to MSA, but not significantly (Table 5.2, Fig. 5.4).

The selected classification tree indicated that period was the factor explaining most variation in normalized densities among studied species, with densities being generally lower in 1995-2010 than in 1977-1986 (Fig. 5.5). Trends for selective grazers (i.e. reedbuck, sable antelope, warthog, and waterbuck) differed from trends of browsers, mixed-feeders, and nonselective grazers (i.e. giraffe, greater kudu, elephant, impala, buffalo, and zebra). For selective grazers, overall densities were not different between MSA

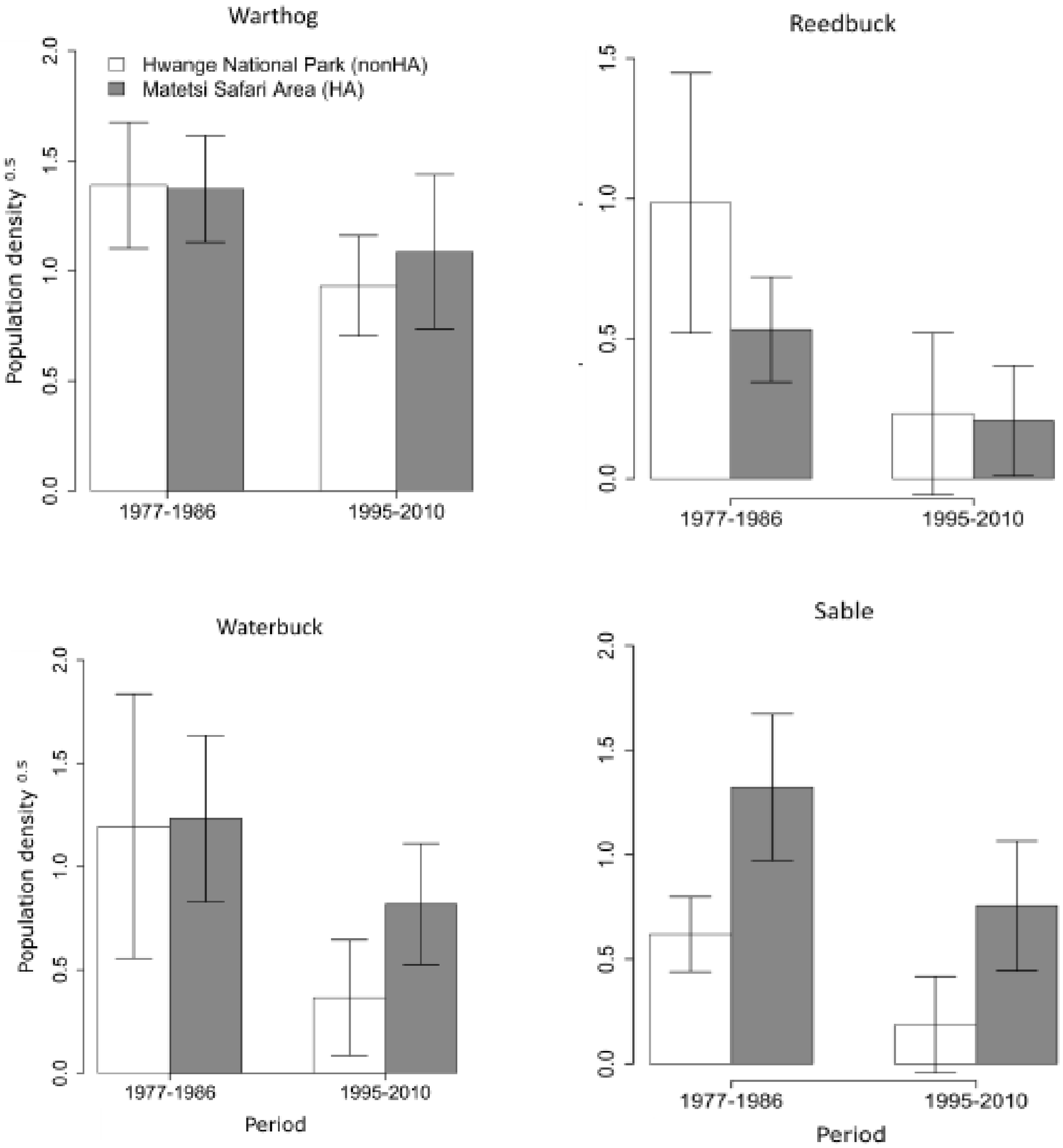
Table 5.2: Two-way analysis of variance of densities (square root-transformed), proportion of adult males (log-transformed) of African ungulate species according to period (1977-1986 *vs* 1995-2010), zone (hunting-free area *vs* hunting areas), and their interaction, in Hwange National Park and the adjacent Matetsi Safari Area, Zimbabwe.

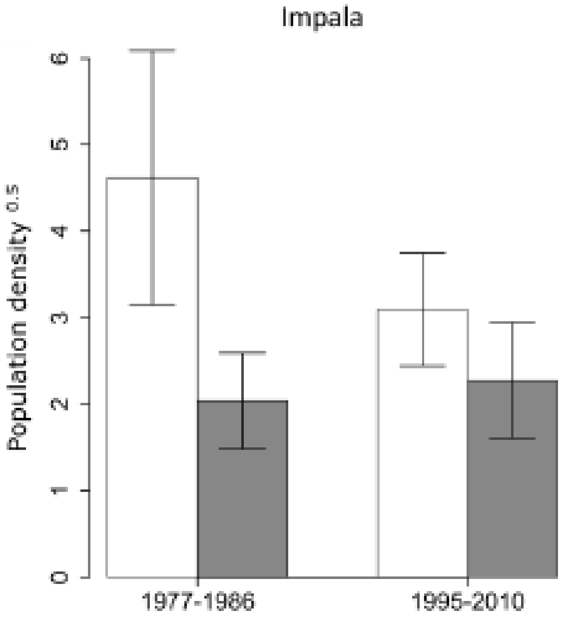
Species	**Factor**	**df** [a]	**Densities**			**Adult males %**		
			rdf [b]	*F*	*P*	rdf	*F*	*P*
Buffalo	period	1	88	0.3	0.6	na [c]	na	na
	zone	1	5	2.8	0.2	na	na	na
	period x zone	1	88	0.6	0.4	na	na	na
Elephant	period	1	88	18.1	0.0001	72	0.1	0.8
	zone	1	5	11.2	0.02	5	7.1	0.04
	period x zone	1	88	2.6	0.1	72	5.4	0.02
Giraffe	period	1	88	1.2	0.3	84	2.8	0.1
	zone	1	5	4.1	0.1	5	4.1	0.1
	period x zone	1	88	26.4	0.0001	84	0.4	0.5
Impala	period	1	87	3	0.1	89	2.5	0.1
	zone	1	5	12.5	0.02	5	2.4	0.2
	period x zone	1	87	25.6	<0.0001	89	2.9	0.1
Greater kudu	period	1	88	1.2	0.3	89	2.4	0.1
	zone	1	5	12.5	0.6	5	0.6	0.5
	period x zone	1	88	25.6	<0.0001	89	0.2	0.7
Reedbuck	period	1	88	31.5	<0.0001	59	0.9	0.3
	zone	1	5	1.1	0.4	5	0	1
	period x zone	1	88	3.6	0.06	59	0.3	0.6
Sable antelope	period	1	88	73.9	<0.0001	73	2	0.2
	zone	1	5	21.4	0.006	5	9.1	0.03
	period x zone	1	88	1.1	0.3	73	6.9	0.01
Warthog	period	1	88	16.6	0.0001	88	0.2	0.6
	zone	1	5	1.3	0.3	5	0.8	0.4
	period x zone	1	88	2	0.2	88	0.6	0.4
Waterbuck	period	1	88	95.2	<0.0001	81	5.3	0.02
	zone	1	5	11.7	0.001	5	5.8	0.06
	period x zone	1	88	1.3	0.3	81	0.3	0.6
Zebra	period	1	88	0.3	0.6	86	3.8	0.0002
	zone	1	5	1.6	0.3	5	14.5	0.06
	period x zone	1	88	2.8	0.1	86	2.7	0.1

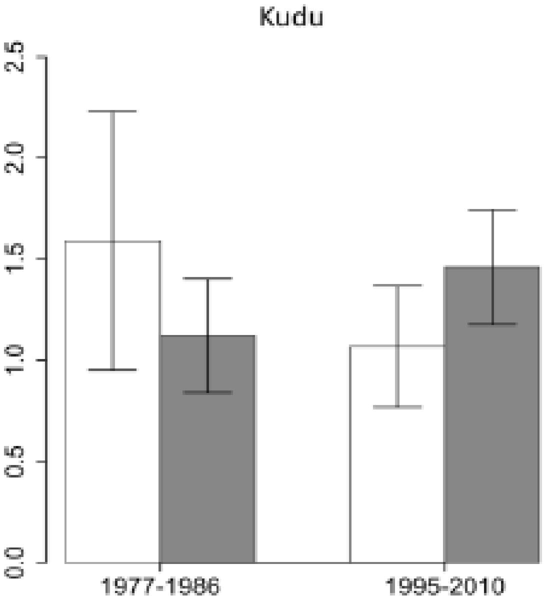
[a] Degrees of freedom.

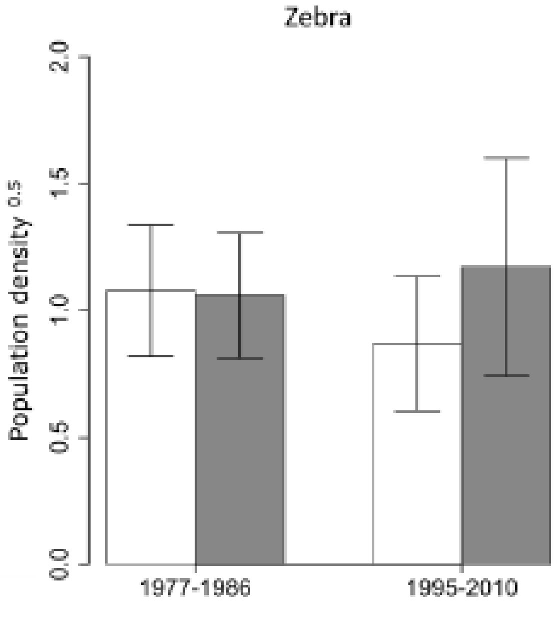
[b] Residual degrees of freedom.

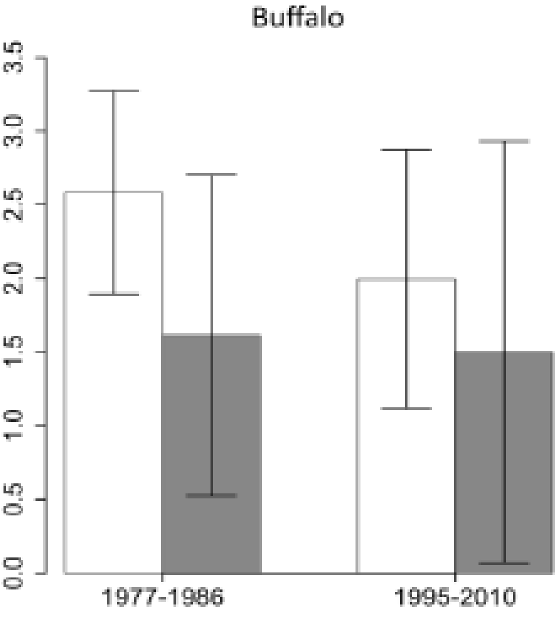
[c] For buffalo, groups were too large to identify individuals.


Warthog
Reedbuck
Waterbuck
Sable
Hwange National Park (nonHA)
Matetsi Safari Area (HA)
Population density 0.5
Population density 0.5
0.0
0.5
1.0
1.5
2.0
1977-1986
1995-2010
Period
Period


Impala
Population density 0.5
0
1
2
3
4
5
6
1977-1986
1995-2010


Kudu
0.0
0.5
1.0
1.5
2.0
2.5
1977-1986
1995-2010


Zebra
Population density 0.5
0.0
0.5
1.0
1.5
2.0
1977-1986
1995-2010


Buffalo
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
1977-1986
1995-2010

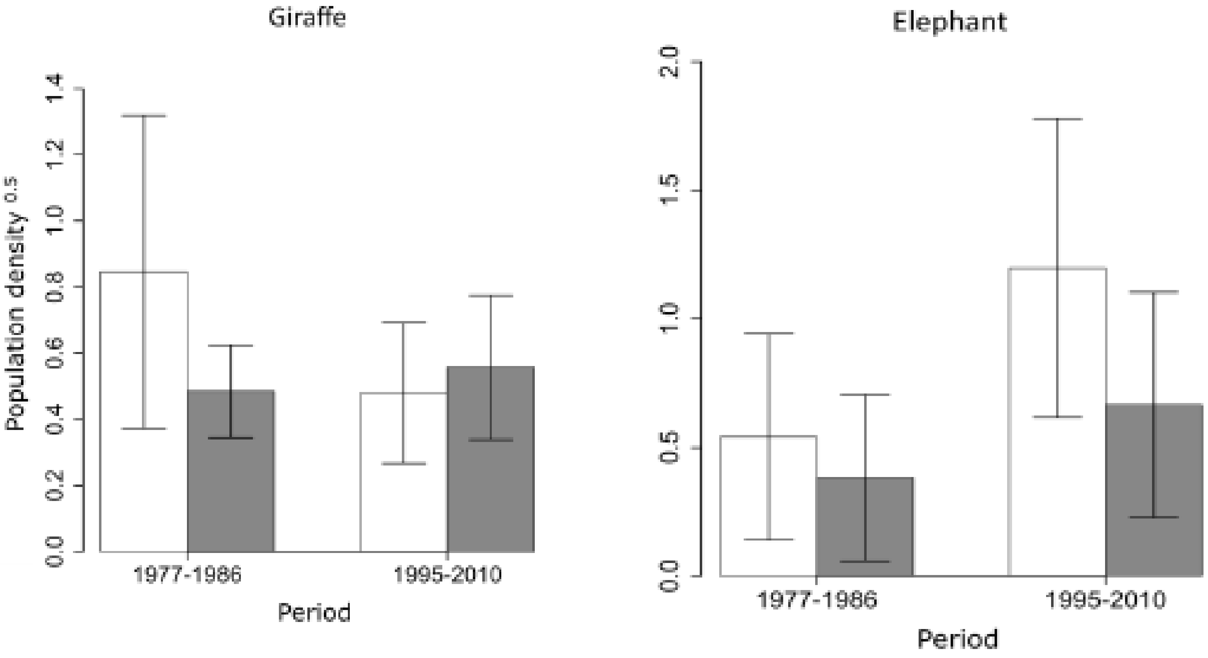


Figure 5.4: Population densities in Matetsi Safari Area (Hunting Areas, HA, grey) vs Hwange National park (hunting-free area, nonHA, white) during 1977-1986 and 1995-2010. The bars indicate the average values and their associated standard deviation.

and HNP, and both zones experienced a decrease in densities of similar magnitude between 1977-1986 and 1995-2010. For browsers, mixed-feeders, and nonselective grazers densities were generally lower in MSA compared to HNP during 1977-1986, more particularly for buffalo, giraffe, impala and greater kudu (Fig. 5.5). However, this difference in densities between MSA and HNP disappeared in 1995-2010 (Fig. 5.5), which indicated a greater decrease of densities in HNP compared to MSA for these species (Fig. 5.5). Elephant and zebra were a distinct subgroup within the group of browsers, mixed-feeders, and nonselective grazers, because their density trends differed from those of the rest of the group (Fig. 5.5). This was consistent with the results from the ANOVA analyses because elephant was the only species whose densities increased during the study period, and zebra did not show any significant spatial pattern or temporal trend of densities.

Proportion of adult males

For sable antelope and elephant, the proportion of adult males was significantly lower in HA than in HNP, and declined in HA between the two periods, whereas not in HNP (Table

5.2; Fig. 5.6). For waterbuck and zebra, this proportion overall declined between the two periods, and tended to be lower in HA compared to HNP (Table 5.2; Fig. 5.6). We found no significant effect of zone, period, or their interaction on the proportion of adult males for the other species (Table 5.2), but this proportion seemed to be lower in HA than in HNP for most of them, more particularly during the period 1995-2010 (Fig. 5.6).

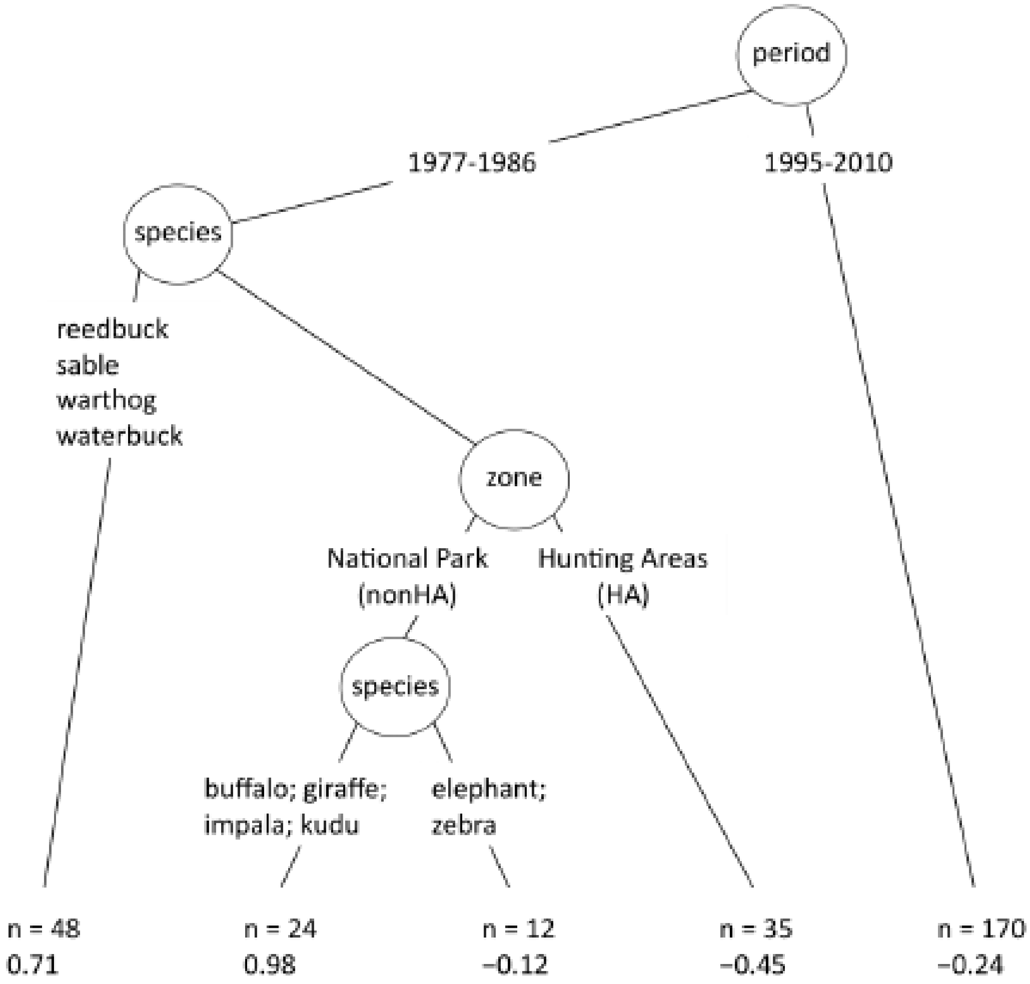
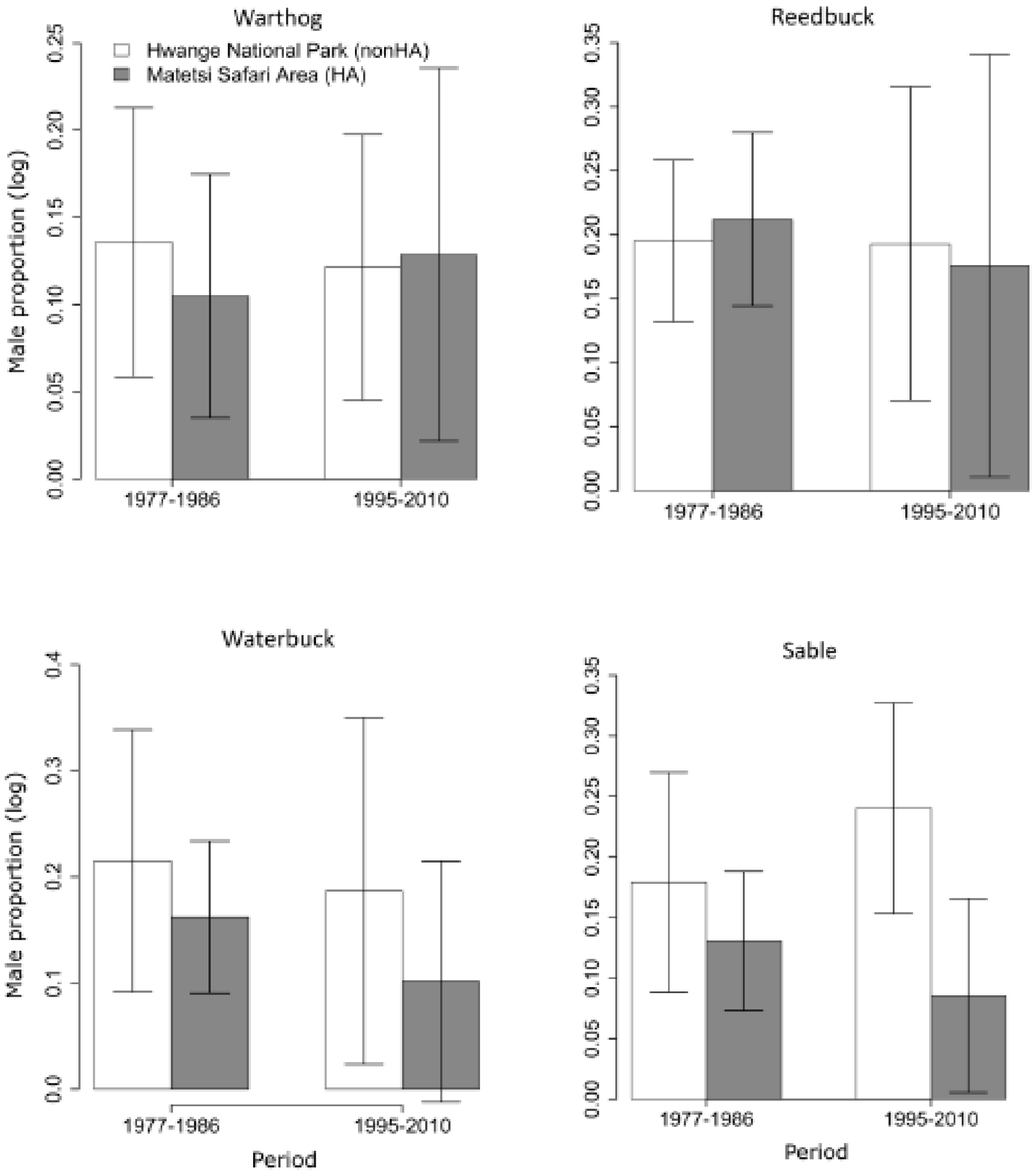
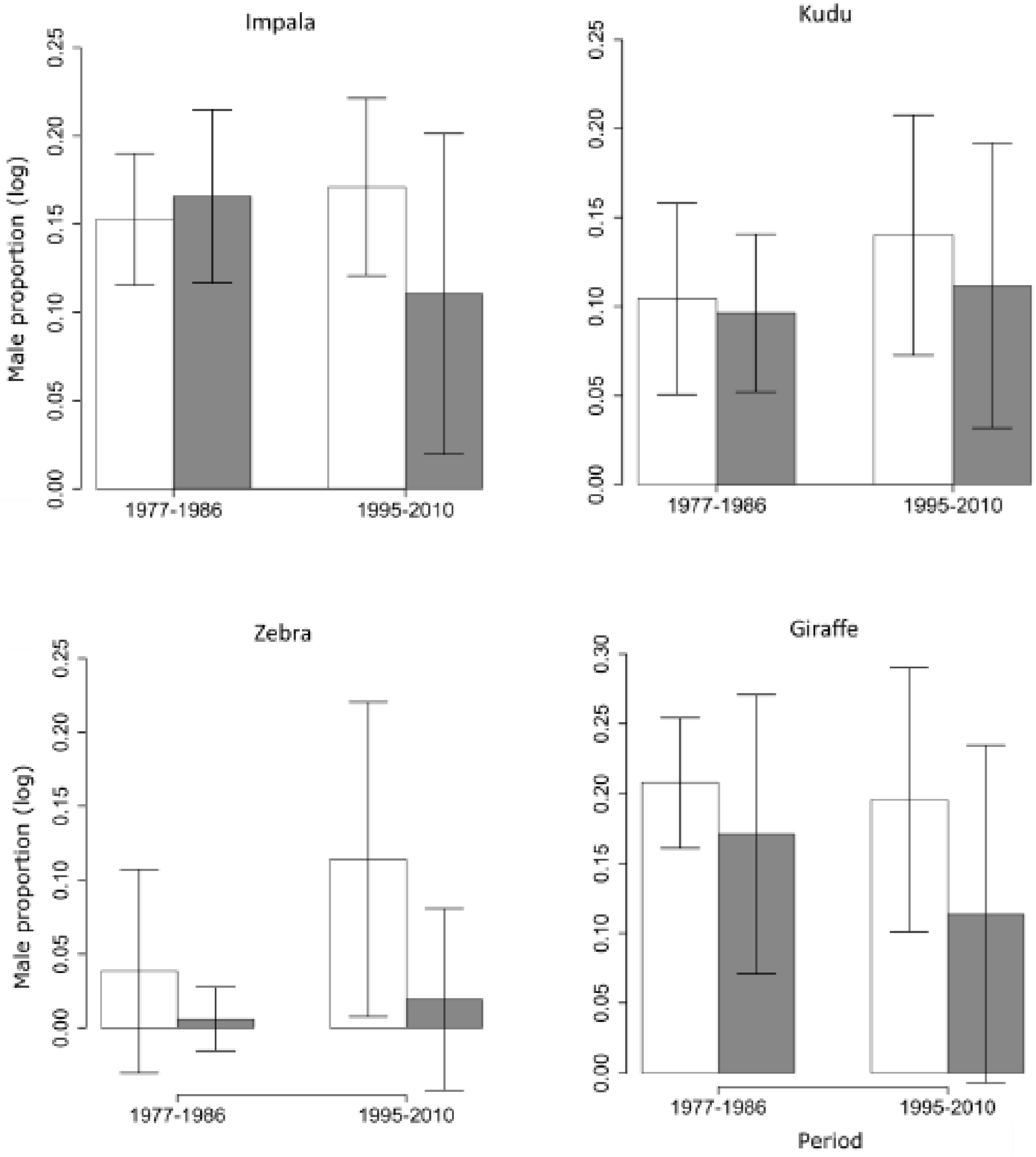


Figure 5.5: Classification tree of the normalized densities according to the zone (National Park vs Hunting Areas), period (1977-1986 versus 1995-2010), and species (buffalo, Burchell's zebra, elephant, giraffe, greater kudu, impala, reedbuck, sable antelope, warthog, waterbuck). Circles are the nodes of the tree. The number of observations (n) and the mean value of normalized densities are indicated and the end of each branch.


Warthog
□ Hwange National Park (nonHA)
■ Matetsi Safari Area (HA)
Male proportion (log)
0.00
0.05
0.10
0.15
0.20
0.25
1977-1986
1995-2010
Reedbuck
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
1977-1986
1995-2010
Waterbuck
Male proportion (log)
0.0
0.1
0.2
0.3
0.4
1977-1986
1995-2010
Period
Sable
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
1977-1986
1995-2010
Period


Impala
Kudu
Zebra
Giraffe
Male proportion (log)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
1977-1986
1995-2010
Period

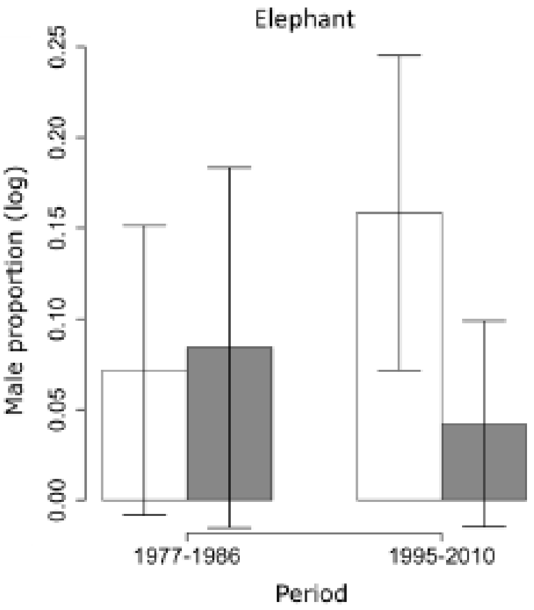


Figure 5.6: Proportion of adult males in Matetsi Safari Area (Hunting Areas, HA, grey) vs Hwange National park (hunting-free area, nonHA, white) during 1977-1986 and 1995-2010. Bars indicate the average values and segments their associated standard deviation.

Discussion

Populations of large herbivores are generally declining in African protected areas (reviewed in Caro et Scholte, 2007; Craigie et al., 2010). This may raise concerns about their efficiency as a conservation tool (Newmark, 2008), and underlines the potential role of alternative zones of conservation such as trophy hunting areas (Lindsey et al., 2007b). However, long-term monitoring of wildlife outside national parks is rare (Caro, 2011). We therefore lack empirical data to investigate the effects of trophy hunting on population structure and density over long periods. This seriously limits our capacity to evaluate the conservation potential of trophy hunting areas. We provide here a rare example of long-term effects of trophy hunting on densities, and proportion of adult males of several large herbivore populations. We compared populations of MSA, Zimbabwe, to populations of the neighbouring HNP over the last 30 years.

Trophy hunting

Overall, trophy hunting had a trivial effect on the spatial patterns and temporal trends of densities and structure of large herbivore populations in the study area. Only elephant and impala showed lower densities in MSA compared to HNP, throughout the study period. Conversely, densities of sable antelope were higher in the hunting areas than in the national park. Under the hypothesis of a detrimental effect of trophy hunting on population densities, we would have expected opposite results because harvest rate was higher for sable antelope than for other species. Harvest rates, however, were generally low in MSA, ca. 2% per year (this study; Cumming, 1989). It is likely that at this level of harvest, the impact of trophy hunting on population densities was minimum. For instance, Caro et al. (1998) found few significant differences in mammal densities between hunting areas and national parks in Tanzania, and suggested that harvest rates below 10% per year were unlikely to impact population sizes. Then, surprisingly for some species (i.e. giraffe, impala, greater kudu), densities declined between 1977-1986 and 1995-2010 in HNP, whereas they did not change or increased in MSA. For species whose densities declined in MSA (i.e. reedbuck, sable antelope, warthog, and waterbuck), there was a decline of similar magnitude in HNP. This suggests that other factors than trophy hunting were responsible for this general decline (see below).

We expected lower proportions of adult males in hunting areas than in HNP because trophy hunting is male-biased (this study; Festa-Bianchet, 2003). For sable antelope and elephant, harvest rates and proportion of males on quotas were higher than for other species. This probably explains why, for these two species in particular, the proportion of adult males was significantly lower in HA than in HNP, and declined in HA between the two periods, whereas not in HNP. For the other species, we overall observed the same trend though not significantly, maybe because of the high variance associated with the proportion of adult males. However, in western Tanzania, Caro (1999b) pointed out that trophy hunting did not necessarily skew the sex-ratio of hunted ungulate populations towards females. Moreover, despite the proportion of adult males tended to be lower and to decline in the hunting areas of our study compared to the national park, the same pattern was not observed in population densities. Studies on Northern ungulates previously reported that the lack of males caused population crashes when harvesting was intense and strongly male-biased (Bergerud, 1974; Freddy, 1987; Milner-Gulland et al., 2003b). Conversely, when harvest rate is low, as it usually is for trophy hunitng, sex ratio is less biased towards females, and there is little evidence of reproductive collapse (reviewed in Milner et al., 2007).

Rainfall

The general decline of population densities between 1977-1986 and 1995-2010 observed in most species across the study area indicated that other factors than trophy hunting were involved. In African savannas, rainfall is a proxy of primary productivity that determines population numbers of large herbivores (Fritz et Duncan, 1994), and annual changes of densities (Mduma et al., 1999). Annual rainfall broadly declined over the last 30 years in the study area. More particularly, the period 1995-2010 followed an unprecedented dry spell decade (Chamaillé-Jammes et al., 2006), i.e. 1986-1994 (Fig. 2), during which dry season rainfall was constantly below the long-term average. Droughts may be particularly detrimental for large African herbivore populations (e.g. Ottichilo et al., 2001; Dunham et al., 2004).

Interestingly, population decline was more pronounced for selective grazers (i.e. reedbuck, sable antelope, warthog, waterbuck) than for nonselective grazers (i.e. buffalo, zebra), mixed-feeders (i.e. elephant, impala), and browsers (i.e. giraffe, greater kudu). This is in accordance with a scenario proposing rainfall as a primary factor determining temporal trends of large herbivore densities in our study area. Browse production is more constant over time than grass production (Rutherford, 1984). Browsers and mixed-feeders are therefore potentially more resistant to droughts than grazers (Hillman et Hillman, 1977; Owen-Smith, 2008), and selective grazers in particular (e.g. Murray et Brown, 1993). In this regard, most examples of large herbivore declines related to droughts in Africa are from grazers (e.g. Mduma et al., 1998; Harrington et al., 1999). Among the selective grazers, warthog experienced a two-fold milder decline than reedbuck, sable antelope, and waterbuck. This is not surprising because warthog can sometimes feed on browse and forbs (Bothma et al., 2004), and is therefore less selective than the three other species.

Natural predation

During the study period, population densities generally declined more in HNP than in MSA. Trophy hunting and rainfall alone are thus not sufficient to explain this result, and we suspect that natural predation might have played a role. Previous studies have pointed out that predators could negatively impact large herbivore populations in African savannas (Sinclair et al., 2003). Between 1971 and the early 1990s, lion (*Panthera leo*), leopard (*Panthera pardus*), and spotted hyaena (*Crocuta crocuta*) numbers have doubled in HNP (Wilson, 1997), but declined afterwards (Drouet-Hoguet, 2007; Loveridge et al., 2007a). Equivalent information does not exist for MSA. However, during this period, large carnivore hunting occurred in MSA at a rate of ca. 8% per year (Cumming, 1989). The removal of adult males in lion and leopard is particularly detrimental for recruitment and population dynamics (Packer et Pusey, 1984; Loveridge et al., 2007a). Therefore, we can assume that densities of lion and leopard remained lower in MSA than in HNP, at least until the mid-1990s. This could be a reason why large herbivore densities generally declined more in HNP than in MSA between 1977-1986 and 1995-2010. Impala and greater kudu are major prey species for most large African carnivores in the region (Drouet-Hoguet, 2007; Loveridge et al., 2007b; Rasmussen, 2009). This may explain why in these species, densities decreased in HNP while they remained constant or increased in MSA. The same argument may be formulated for giraffe that is a common prey of lion in Hwange (Loveridge et al., 2007b). The pattern tended to be the same for buffalo and zebra, two other major preys of lion in Hwange (Loveridge et al., 2007b), though not significantly. Conversely, for selective grazers, the difference in temporal trends of densities between HNP and MSA was less contrasted, possibly because rainfall was the primary driver of trends in densities for these species.

Elephant

Elephant was the only large herbivore species whose densities increased in both zones during the study period. Chamaillé-Jammes et al. (2008) previously showed that elephant numbers in HNP drastically increased from 15,000 to 35,000 since the cessation of culling in 1986. Elephant densities increased in both zones, but remained higher in HNP compared to HA throughout the study period. This is coherent with elephant behaviour, because elephants tend to avoid human-disturbed areas (van Aarde et al., 1999; Caro, 1999b). High elephant densities are suspected to be detrimental for other large herbivores, because of habitat modification and competition for scarce resources (Cumming, 1982; Valeix et al., 2007a), but this is still largely debated (Skarpe et al., 2004; Valeix et al., 2009c). Further investigation is still required to conclude on whether temporal trends and spatial patterns of elephant densities could be partly responsible for the greater decline of large herbivore densities in HNP compared to the neighboring MSA during the study period.

Our study illustrates that when removal is rather conservative and rigorously managed, trophy hunting areas may be valuable conservation zones for large herbivores. However, natural factors such as predators and elephant may have obscured the effect of trophy hunting on spatial and temporal trends of herbivore densities in our study area. Indeed, human disturbance may inderectly benefit prey by displacing their predators (Berger, 2007; Leighton et al., 2010; Muhly et al., 2011). Thus, hunting areas of MSA might have acted as refuges from predators, and possibly elephants. Fine-scale spatial variations in rainfall regime may also have partly accounted for the differences in herbivore densities between MSA and HNP. This remains to be investigated. Given the actual recurrence of long and severe dry episodes in southern Africa (Hulme et al., 2001; Nicholson 2001), selective grazers may deserve a particular focus in hunting areas because they may be less able to cope with additional sources of mortality than droughts compared to nonselective grazers, browsers, and mixed-feeders.

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Environmental Research Development), as well as with the Research Platform “Production and Conservation in Partnership” RP-PCP, funded by the French “Ministère des Affaires Etrangères”, “Ambassade de France au Zimbabwe”, CIRAD, CNRS and the IFB “Global Change and Biodiversity”. We thank S. Le Bel, CIRAD representative in Zimbabwe. We are indebted to Tawanda Tarakini, Peter Makumber, Tsitsi-Theone Maponga, Gugulethu Ncube, Bertrand Eliotout, Hugo Valls, and Stéphanie Périquet, who completed data entry of the road count folders.

CHAPITRE 6
L'HIPPOTRAGUE NOIR, ENTRE L'HOMME ET L'ÉLÉPHANT

Human-elephant interference may promote densities of a rare antelope in elephant-dominated African savannas

WILLIAM-GEORGES CROSMARY, SIMON CHAMAILLÉ-JAMMES, GODFREY MTARE, STEEVE D. CÔTÉ, HERVÉ FRITZ

En révision dans « Biodiversity and Conservation ».

Résumé

L’augmentation actuelle des populations humaines en Afrique sub-saharienne affecte la vie sauvage, particulièrement autour des aires protégées. Egalement, les densités d’éléphant *Loxodonta africana* ont considérablement augmenté dans les aires protégées d’Afrique australe au cours des deux dernières décennies, possiblement au détriment des autres herbivores. Nous avons utilisé des données de suivis à long terme conduits dans l’écosystème Hwange où il existe un gradient de perturbation humaine et de densités d’éléphants dans le nord ouest du Matabeleland, Zimbabwe, pour examiner les variations spatiales et temporelles de l’hippotrague noir *Hippotragus niger*, une antilope rare et emblématique de la région. Comme attendu, les densités d’hippotrague noir étaient très basses sur les terres communales, zones les plus anthropisées. Elles étaient curieusement élevées dans les zones de chasses et les forêts d’état, alors que plus basses et en déclin dans le Parc National de Hwange. Les conditions environnementales (i.e. disponibilité en eau de surface, type de végétation, et abondance de compétiteurs) étaient semblables entre le parc national et sa périphérie, et n’ont donc pas pu être à l’origine de ce résultat surprenant. Les éléphants en revanche ont répondu comme attendu à la perturbation humaine, avec des densités plus basses à l’extérieur du parc national. Ces résultats suggèrent un effet indirect de la perturbation humaine sur les densités d’hippotrague noir modulé par le fait que les éléphants évitent les zones perturbées par l’Homme. Nous pensons que cette étude est un exemple de la façon dont une espèce subordonnée peut s’accommoder d’un niveau intermédiaire de perturbation humaine pour atténuer les effets négatifs associés à la présence d’une espèce dominant surabondante.

Abstract

The recent ongoing increase of human populations in sub-Saharan Africa impacts wildlife, especially around protected areas. Simultaneously, elephant *Loxodonta africana* densities have remarkably increased in protected areas of Southern Africa in the last two decades. Concerns have been raised that elephants may be increasing at the expense of other herbivore species. We used long-term censuses conducted over the Hwange ecosystem, a gradient of human disturbance, and elephant densities in northwest Matabeleland, Zimbabwe, to investigate spatial and temporal variations in densities of a rare and emblematic ungulate, the sable antelope *Hippotragus niger*. As expected, sable antelope densities were very low in communal lands, the most disturbed areas. They surprisingly thrived in hunting areas and forest lands, whereas their densities were much lower, and even declined, in Hwange National Park. Environmental conditions (i.e. availability of surface water, vegetation type and quality, and abundance of competitors) were unlikely to account for the unexpected distribution of abundance of sable antelopes, because we detected no difference in environmental conditions between the Park and its surroundings. Elephants responded as expected to disturbance, with much lower densities outside the Park than inside. These results suggest an indirect effect of human disturbance on sable antelope densities modulated by the avoidance of human-disturbed areas by elephants. We believe this is an example of how subordinate species may accommodate intermediate levels of human disturbance to mitigate the strong negative influence of an overabundant "keystone" species.

Keywords: sable antelope, elephant, African savannas, land use, human disturbance.

Introduction

With the ongoing increase of human populations, and the consequent spread of human encroachment over natural habitats, there is growing concern about how wildlife is impacted by human disturbance (e.g. Prins, 1992; Cleaveland et al., 2001; Fritz et al., 2003; Milner-Gulland et Bennett, 2003a). In many African countries, large areas have been set aside to protect wildlife from human expansion. Some protected areas, such as National Parks, strictly prohibit human activities (excepted viewing tourism), and resource extraction within their boundaries (IUCN categories I-III *sensu* WRI/UNEP/UNDP/WB, 1996). These "strictly" protected areas have long been assumed to offer the best legal protection for wildlife (Campbell et Hofer, 1995). It is gradually acknowledged, however, that the existence of these protected areas alone is not sufficient to guarantee the conservation of wildlife (reviewed in Newmark, 2008).

The future of wildlife conservation stretches outside these protected areas, where the majority of most large mammal populations occurs, and needs to be protected (Fjeldsa et al., 2004; Western et al., 2009). Conservation outside National Parks mostly relies on the establishment of partially protected areas (IUCN categories IV and V *sensu* WRI/UNEP/UNDP/WB, 1996), usually located at the periphery of National Parks, and acting as buffer zones reducing human expansion. These partially protected areas allow diverse forms of wildlife utilization to offset the costs associated with the protection of wildlife and natural habitats. Contrary to National Parks, they harbour consumptive activities ranging from exclusive hunting tourism on state or private lands, to a combination of hunting tourism, local hunting, timber harvesting, livestock, and subsistence cropping on forestry areas and communal lands. Wildlife in African savannas is thus spread across a mosaic of areas with contrasting land uses, management practices, densities of people and livestock. Thus, it is crucial to understand how anthropogenic factors, in addition to abiotic and biotic factors, affect the demography of wild populations.

Long-term monitoring and research programs previously reported that large herbivore populations in semi-arid African savannas are naturally influenced by rainfall and primary production (Coe et al., 1976; Fritz et Duncan, 1994), availability and distribution of surface-water (Redfern et al., 2003; Ogutu et al., 2010), and predation (Sinclair et al., 2003;

Fritz et al., 2011). In addition, the remarkable increase of elephant *Loxodonta africana* populations across southern Africa in the past decades (Blanc et al., 2005), may have negatively affected the populations of other large herbivores through habitat modification (e.g. loss of woodlands, Cumming, 1982), or competition for scarce resources (e.g. surface water, Valeix et al., 2007a). However, negative impacts of elephants do not always appear to be the rule (Skarpe et al., 2004; Valeix et al., 2009c). Most investigations took place in National Parks, and it thus remains uncertain how human disturbance may interact with other factors, such as elephants, to determine the abundance of herbivores. For instance, if human disturbance negatively affects elephant densities in areas outside National Parks, other large herbivores that may suffer from high elephant densities could then be released from elephant pressure in these areas.

Sable antelope *Hippotragus niger* is an emblematic large herbivore, and an important species in ecotourism and hunting industries of Southern Africa (Lindsey et al., 2007b). Sable antelope populations are nowadays mainly confined to protected areas, and to some private lands of Southern Africa. Zimbabwe, and particularly the Hwange ecosystem, hosts some of the highest densities of sable antelope (East, 1999). Here, we used long-term data from aerial surveys conducted over the Hwange ecosystem, from 1990 to 2001 to explore spatiotemporal trends of sable antelope densities across a variety of land uses, i.e. a National Park, state-owned hunting areas, forest and private lands, and communal lands. We assessed the effect of human disturbance on sable antelope densities concomitantly with environmental variables, i.e. distribution of surface water, vegetation (types and quality), and abundance of competitors (besides elephant). Chamaillé-Jammes et al. (2008) previously showed that elephant numbers in Hwange National Park more than doubled since the cessation of elephant culling in 1986. Sable antelope may be particularly sensitive to high elephant densities, because they strongly depend on wooded habitats (Estes, 1991), such resource being possibly jeopardized by high elephant densities (Cumming et al., 1997; O’Connor et al., 2007; Guldemond et van Aarde, 2008). We thus also included the trend in elephant numbers across this ecosystem in our analysis. Because we suspected that human disturbance may act as a deterrent factor for elephants, hence limiting their increase outside the Park, we hypothesised that the positive effect of lower elephant densities outside the Park may reduce the negative effect of human disturbance on sable densities in partially protected areas. We predicted that (i) elephant densities would decline along the gradient of human disturbance, whereas (ii) sable antelope densities should increase because of lower elephant densities. At high human disturbance however, both elephant densities and sable densities should be low. In Hwange National Park, since cessation of elephant culling, (iii) elephant densities should increase with years, whereas sable antelope densities should concomitantly decline. We discuss the relative effects of land use and elephant densities on sable antelope densities across the Hwange ecosystem, and the implications for conservation.

Material and methods

Study site

The study was conducted in Hwange National Park and surrounding areas (between 17°45'S-20°30'S and 25°15'E-28°00'E), ca. 37,000 km^2, in northwest Zimbabwe, Matabeleland province (Fig. 6.1). This area is the key Zimbabwean component of the Kavango Zambezi Transfrontier Conservation Area, an interconnected mosaic of protected areas, partially protected areas, and transboundary wildlife corridors shared by Angola, Botswana, Namibia, Zambia, and Zimbabwe. In this ecological complex, sable antelope has been identified as one of the species requiring special attention (Peace Parks Foundation, 2009). The Hwange ecosystem covers diverse types of land uses, i.e. a National Park, state-owned hunting areas, private hunting areas, Forestry lands, and communal lands. This offers the possibility to investigate trends in sable numbers along a gradient of human disturbance (Table 6.1, Fig. 6.1) (further information on land types is provided in Appendix 6.1).

Some of the environmental variables, i.e. rainfall, temperature, soil characteristics, and availability of surface water, change along a latitudinal gradient across the Hwange ecosystem (Peace Parks Foundation, 2009). To disentangle the effects of these environmental variables from those of land use, we restricted our study area to the central region of Hwange ecosystem, excluding the southern part of HNP, and the northern part of MSA (Fig. 6.1). However, we kept Tsholotsho in the study area, because this is the only

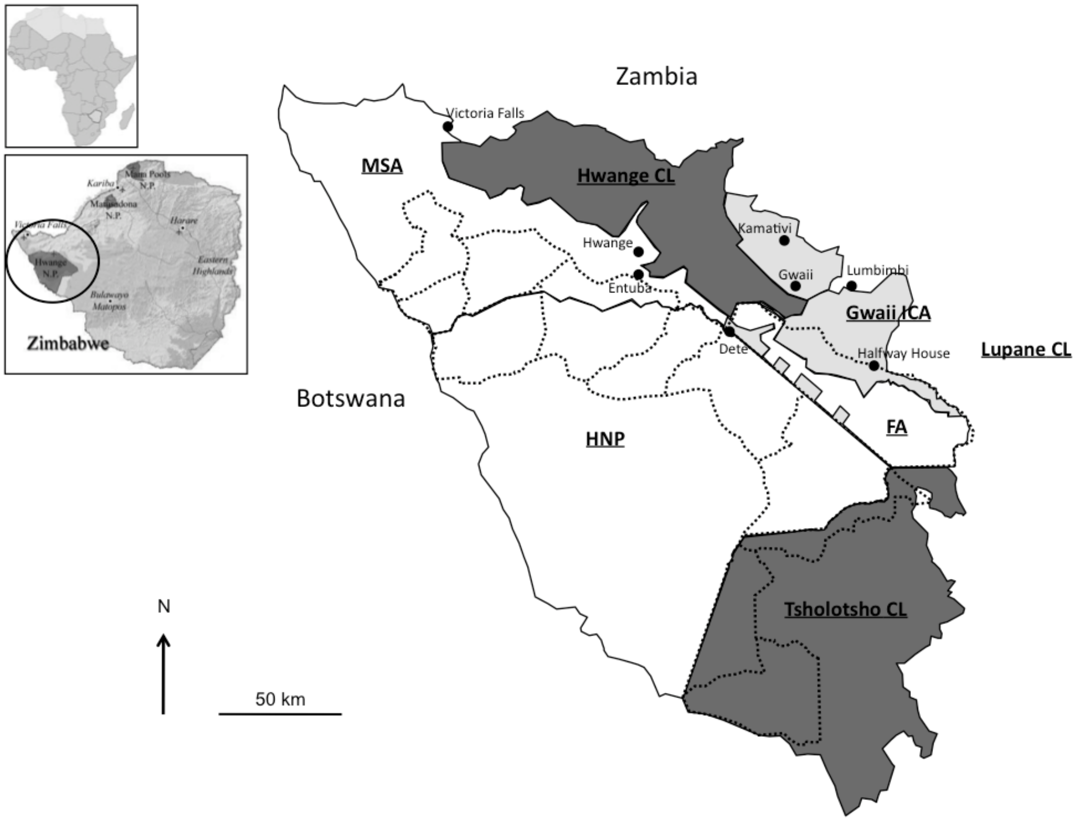

Figure 6.1: Hwange National Park (HNP) and immediate surrounding areas, i.e. Matetsi Safari Area (MSA), Gwaii Intensive Conservation Area (Gwaii ICA), Forestry Areas (FA), and communal lands (CL), in Zimbabwe. Different color tones identify different land uses, i.e. white for state lands, light gray for private lands, and dark gray for communal lands. The dashed black line delineates the study area. Dots represent locations of the principal towns and villages.

communal land adjacent to HNP. The Hwange ecosystem receives an annual average of 650 mm of rainfall from November to April. Natural water is associated with pans, springs, vleis, and pools in rivers and streams. Most water sources are seasonal, and eventually dry up early in the dry season. Water during the dry season is mainly available in artificial waterholes. Vegetation is typical of southern African dystrophic wooded and bushed savannas with patches of grasslands (Rogers, 1993; Ganzin et al., 2008). Well-drained shallow rocky soils characterize MSA and the northwestern part of HNP, but poorly drained clayey soils occur more to the east. Vegetation in the northwestern part of HNP is dominated by *Colophospermum mopane* and *Combretum spp.* (Ganzin et al., 2008). Poorly drained Kalahari sands characterize the northeastern part of HNP and FA/Gwaii. *Baikiaea plurijuga*, *Burkea africana*, and *Terminalia sericea* dominate the vegetation there, with more *Brachystegia* woodlands in FA/Gwaii than in HNP (Ganzin et al., 2008). Tsholotsho mostly lies on Kalahari sands and hosts a vegetation dominated by *Acacia-Baikiaea* woodlands (Ganzin et al., 2008).

Table 6.1: Categories of land use and associated land tenure across Hwange ecosystem, Zimbabwe, arranged along an increasing gradient of human disturbance. Areas of studied areas within each land use are indicated, as well as the number of sampled aerial blocks.

Area	**Land use**	**Land tenure**	**Human disturbance**	**Human disturbance gradient**	**Studied superficies (km²)**	**Aerial blocks (number)**
Hwange National Park	National Park	State-Zimbabwe Parks and Wildlife Management Authority	Viewing tourism	↓	5,800	5
Matetsi Safari Area	Hunting area	State-Zimbabwe Parks and Wildlife Management Authority	Viewing tourism Hunting tourism		2,200	3
Forest Area / Gwaii Intensive Conservation Area	Forest / Hunting area	State-Forestry Commission / Private lands	Viewing tourism Hunting tourism Limited human settlement Logging Livestock Poaching		3,100	2
Tsholotsho	Communal Lands	Communities	Viewing tourism Hunting tourism Human settlements Subsistence agriculture Legal local hunting Logging Livestock Poaching		3,100	3

Aerial census data

ZPWMA and the World Wildlife Fund for Nature (WWF) conducted aerial strip-transect censuses in the North-Matabeleland each year during the dry season, from 1990 to 2001 (except in 2000) (Reports available at the WWF Regional Office). Censuses followed the procedure recommended by Norton-Griffiths (1978) and were analysed using the Jolly's method (1969). For each aerial block sampled (Fig. 6.1 and Table 6.1), population densities were estimated annually for sable antelope, its potential competitors (i.e. African buffalo *Syncerus caffer*, plains zebra *Equus burchelli*, and blue wildebeest *Connochaetes taurinus*; according to Chirima, 2010), and elephant. We excluded 1992 and 1998 because the block design was different from other years.

Environmental variables

We calculated the availability of surface water as the proportion of area in each block located within 5 km from any potential surface water supply during the dry season. Wooded habitats were also expressed as the proportion of area within each block, which we assumed to be relatively constant throughout years within blocks (the proportion of the principal vegetation types are given in Appendix 6.2).

We used the satellite-derived normalized difference vegetation index (NDVI) as a proxy of vegetation productivity (Petorrelli et al., 2005). We used 10-day NDVI images (resolution 1.2 x 1.2 km) derived from 1990 to 2001 from Advanced Very High Resolution Radiometer/National Oceanographic and Atmospheric Agency satellites. The Institute for Soil, Climate, and Water, from the South African National Agricultural Research Council, provided NDVI images. We summed the 10-day NDVI images from October to May (included), corresponding to the rainy season, for each year, and then averaged NDVI value per year for each block.

As a proxy of competition we calculated the total metabolic biomass of potential competitors for sable antelope (buffalo, plains zebra, and wildebeest) using reference metabolic body mass (Cumming et Cumming, 2003) and population estimates from the aerial censuses. Calculations were made for each year within each block.

Statistical analyses

Because our data set did not comprise enough years (n=8), we could not test simultaneously in a model the effect of land use on sable antelope densities with the co-variables, i.e. year, elephant densities, surface water, wooded habitats, NDVI, and abundance of competitors. We thus performed two analyses: i) one focusing on the effect of land use on average sable antelope densities (i.e. mean densities between 1990 and 2001); ii) the other on the temporal trends of sable antelope densities within each land use. Because no sable antelope were observed in Tsholotsho during the study period, we removed it from the aerial census analyses.

Spatial pattern of densities and environmental variables across Hwange ecosystem

We used the nonparametric Wilcoxon test to investigate whether there was any correlation between land use and environmental variables. Because FA/Gwaii had only 2 blocks sampled (Fig. 6.1), we regrouped them with the 3 blocks of MSA to test for differences between the National Park and the surrounding land uses. We then tested for any effect of land use on elephant averaged densities and on sable antelope averaged densities using the nonparametric Wilcoxon test.

Temporal trends of ungulate densities across Hwange ecosystem, 1990-2001

We explored temporal trends of sable antelope densities in parallel to trends in elephant densities by regressing along years, in each land use: (i) elephant densities, and (ii) sable antelope densities. We initially used linear mixed-effect models with NDVI and competitors abundance as random factors. In all models, random factors did not modify the results of the analyses. We consequently simplified the models to linear fixed-effects models.

Results

Land use and environmental variables

Environmental variables did not change with land use because we observed no difference in the availability of surface water (Wilcoxon test, $W = 10$, $P = 0.7$), wooded habitats ($W = 14$, $P = 0.8$) (see the proportion in Appendix 6.2), NDVI ($W = 15$, $P = 0.7$), and abundance of competitors ($W = 15$, $P = 0.7$) between HNP and MSA/FA/Gwaii.

Aerial censuses: spatial pattern of densities across Hwange ecosystem

The averaged elephant densities significantly changed with land use (Wilcoxon test, $W = 25$, $P < 0.01$), with densities ca. four times higher in HNP than in MSA/FA/Gwaii (Fig. 6.2a). Within MSA/FA/Gwaii, densities tended to be lower in FA/Gwaii than in MSA, but these values could not be statistically tested because of the low number of blocks in FA/Gwaii.

The averaged densities of sable antelope also significantly changed across land uses ($W = 0$, $P < 0.01$), with densities ca. four times lower in HNP than in MSA/FA/Gwaii (Fig. 6.2b). Within MSA/FA/Gwaii, sable antelope densities tended to be lower in MSA compared to FA/Gwaii (Fig. 6.2b), but we could not test it statistically because of the low number of blocks in FA/Gwaii.

Aerial censuses: temporal trends of densities across Hwange ecosystem, 1990-2001

None of the land uses experienced any temporal trend in elephant densities during the study period (HNP: year, $F_{1,7} = 0.9$, $P = 0.4$; MSA: year, $F_{1,7} = 1.8$, $P = 0.2$; FA/Gwaii: $F_{1,7} = 1.8$, $P = 0.2$) (Fig. 6.3a). Sable densities declined with years in HNP (estimate ± SE, -0.023 ± 0.006, $F_{1,7} = 15.4$, $P < 0.01$), while no significant trend was observed in MSA (year, $F_{1,7} = 0.6$, $P = 0.4$), or FA/Gwaii (year, $F_{1,7} = 0.7$, $P = 0.4$) (Fig. 6.3b).

Discussion

We analysed trends of sable antelope densities across Hwange ecosystem in Zimbabwe, a mosaic of land uses (i.e. National Park, state owned hunting areas, forest and private lands, and communal lands), in conjugation with environmental variables, and elephant densities. Land use influenced the spatial distribution of sable antelope densities. Communal lands, as expected, hosted the lowest densities of sable antelope. Several studies previously pointed out the scarcity of wildlife across African human-dominated landscapes. In the mid-Zambezi Valley for instance, a nearby ecosystem in Zimbabwe, Fritz et al. (2003) showed that the richness and diversity of large herbivores decreased with expansion of agricultural fields subsequent to the eradication of the Tse-Tse fly (*Glossina* spp.). Similarly, in western

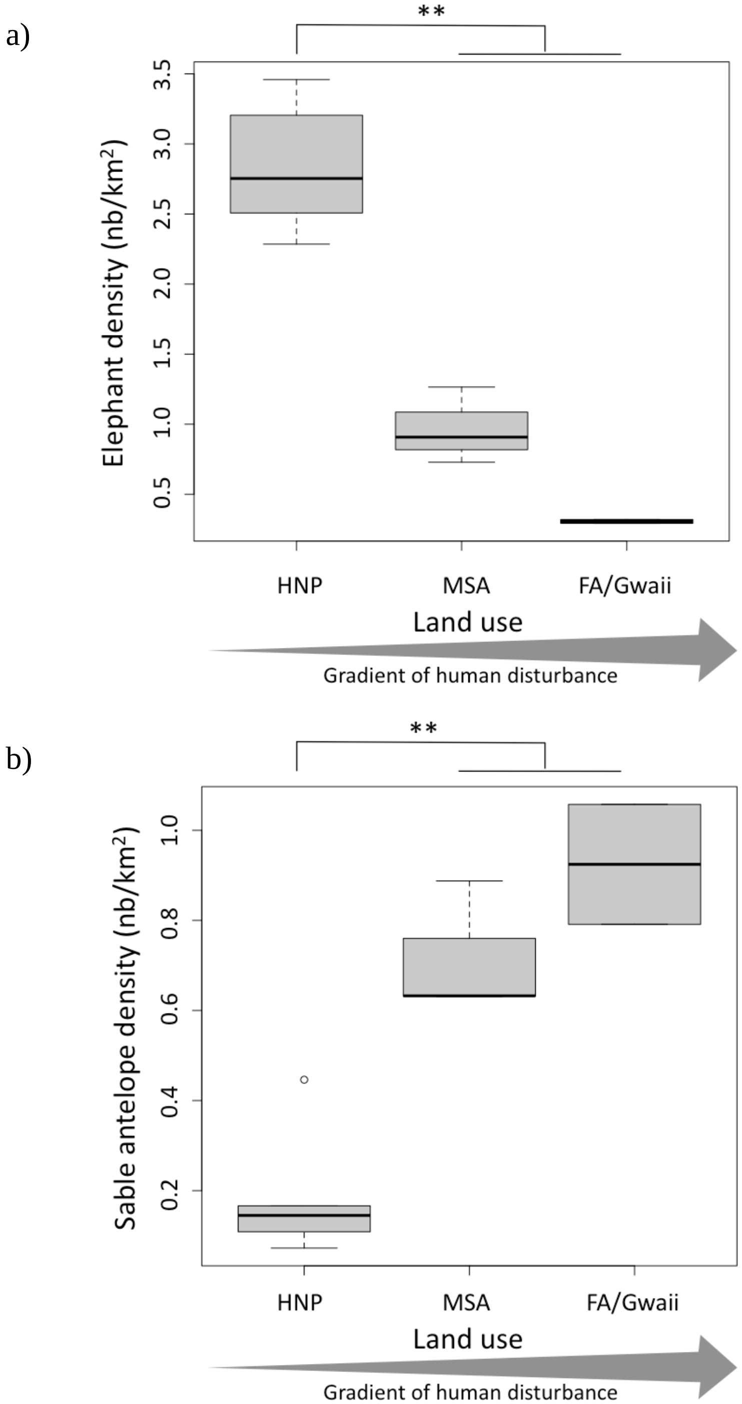

Figure 6.2: Effect of land use on (a) elephant densities, and (b) sable antelope densities, across Hwange ecosystem (Zimbabwe). Box plots represent densities averaged over the study period, from 1990 to 2001, in the northern part of Hwange National Park (HNP), the southern part of Matetsi Safari Area (MSA), and Forest and Gwaii ICA private lands (FA/Gwaii). Averaged densities are compared among land uses. ** $0.005<P< 0.01$. Although we grouped the 2 blocks of FA/Gwaii with the 3 blocks of MSA for the analyses, we present the two land uses separately in the figure because they graphically differ from each other.

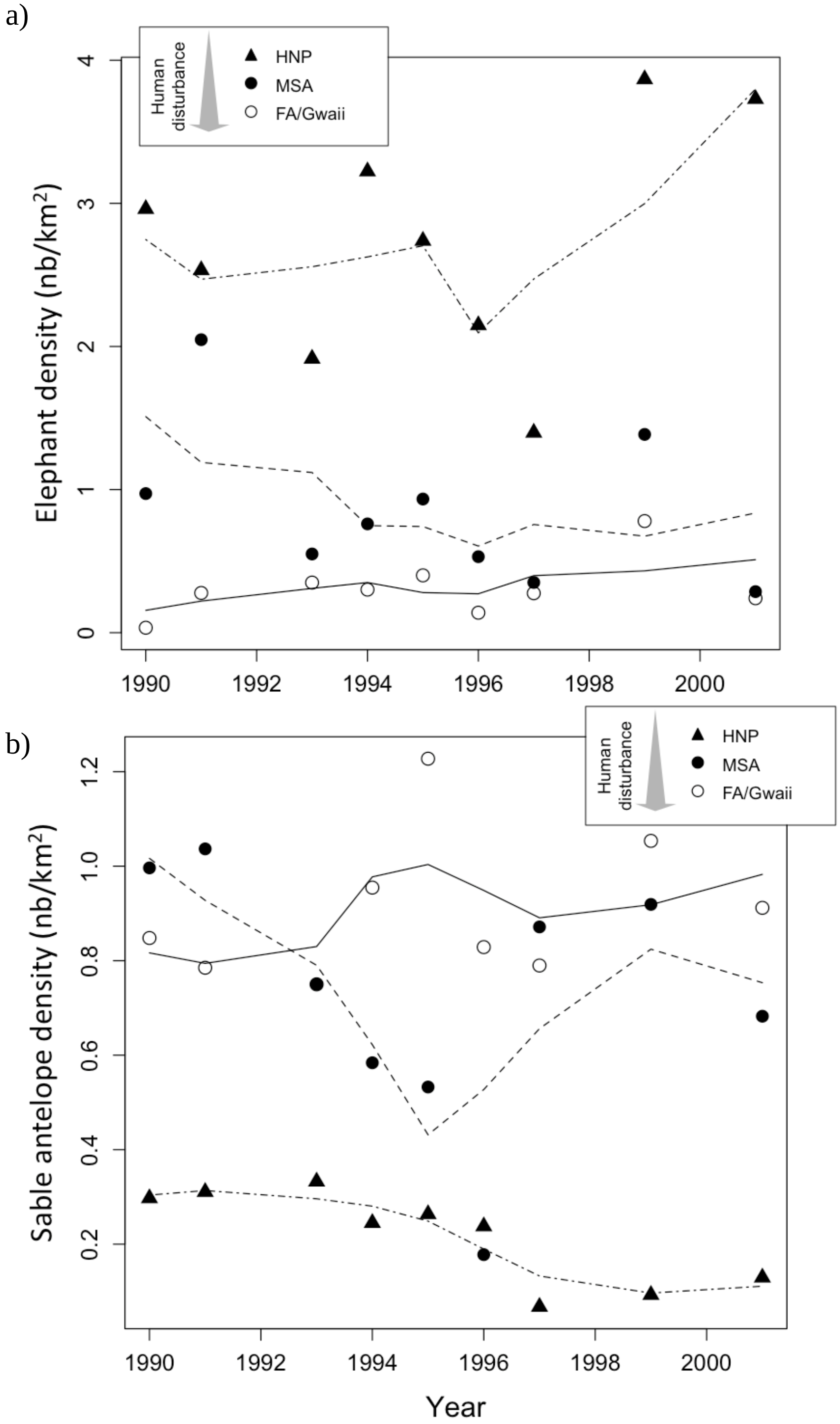

Figure 6.3: Temporal trends of (a) elephant densities, and (b) sable antelope densities, from 1990 to 2001, under different land uses across Hwange ecosystem (Zimbabwe): northern part of Hwange National Park (HNP), southern part of Matetsi Safari Area (MSA), Forest and Gwaii private lands (FA/Gwaii). Data points indicate annual values of densities, lines the 3-year running averages (mean of years n-1, n and n+1). Dashed lines are used for non-significant trends.

Tanzanian Open Areas, equivalent to the communal lands of our study, Caro (1999c) observed that wildlife densities were generally much lower than in the neighbouring protected areas. Some wild herbivores, however, e.g. plains zebra and Grant's gazelle (*Nanger granti*) in Kenya, showed resilience to human and livestock presence (Georgiadis et al., 2007). Sable antelope groups, however, are territorial and present a well defined social structure (Estes, 1991), which makes them particularly sensitive to displacements imposed by human and livestock. They furthermore access surface water preferentially during daytime (Valeix et al., 2007a), and thus are also less likely to visit waterholes at night (when livestock are paddocked in general) unlike plains zebra and Grant's gazelle. Sable antelope are also specialized grazers that preferentially feed on foliage and herbs (Estes, 1991), and so would hardly cope with forbs and shrubs at livestock-disturbed sites (but see Grobler, 1974, for sable antelope at Matopos National Park, Zimbabwe). Finally, as a woodland species, sable antelope may be particularly exposed to poaching by snaring, and to changes in canopy cover due to wood harvesting and charcoal production in human-dominated landscapes. So the absence of sable antelope in the communal lands around Hwange National Park was expected.

More surprisingly, however, sable antelope densities were ca. four times lower in Hwange National Park than in Matetsi Safari Area (i.e. state hunting area) and Forestry/Gwaii Area (i.e. forest lands and private hunting area). And outside the Park, densities of sable antelope tended to be higher in Forestry/Gwaii Area than in Matetsi Safari Area. Thus, with the exception of communal lands, sable antelope densities unexpectedly increased along the gradient of human disturbance. Whether human activities in Matetsi Safari Area and Forestry/Gwaii Area disturbed sable antelope populations may then be questioned. For Lindsey et al. (2007a), trophy hunting is self-regulated because excessive harvest rates negatively affect trophy quality, which eventually reduces the number of clients interested in hunting. Over-harvesting risk is thus limited. In the 1990s, legal off-take rates in hunting areas around Hwange National Park ranged from 0 to 5% of estimated sable antelope population sizes, with extremes at 9% (Cumming, 1989; ZPWMA Unpublished data). In Tanzania, Caro et al. (1998) suggested that below 10% of the population size, legal hunting would be sustainable for most large herbivore populations. This may explain why we did not detect any negative trend in densities of sable antelope in

Matetsi Safari Area, nor in Forestry/Gwaii Area. Thus, trophy hunting per se, when well regulated, has probably only a limited impact on densities of harvested populations (e.g. in Kativi ecosystem, Tanzania, Caro et al., 1998). This hypothesis alone, however, cannot explain why we observed higher densities of sable antelope in Matetsi Safari Area and Forestry/Gwaii Area than in Hwange National Park.

In Zimbabwe, hunting can generate up to 30 times more revenues than photographic tourism (Chardonnet, 1995), hence possibly justifying a greater investment in management actions as well as protection of wildlife in hunting areas (Lewis et Alpert, 1997; Caro, 1999c; Lindsey et al., 2007b), as anti-poaching effort and surface water supply. Anti-poaching remained, however, very effective in Hwange National Park during the 1990s (ZPWMA, Unpublished data). Likewise, ZPWMA actively managed surface water by developing artificial waterholes between the 1930s and the early 1980s in Hwange National Park to maintain supply of surface water throughout the dry season. In general, environmental features did not contrast between Hwange National Park and the surrounding hunting areas or forest lands. We did not detect any significant difference in the (i) availability of surface water, (ii) availability of wooded habitats, (iii) NDVI indices, and (iv) averaged densities of forage competitors. NDVI and the abundance of competitors, moreover, did not influence temporal trends of sable densities within the different land uses. Consequently, neither differences in management efficiency, nor environmental variables could have been responsible for the higher densities of sable antelope observed outside Hwange National Park than in the Park.

Predation has been suggested to be a major determinant in the decrease of roan antelope *Hippotragus equinus* (Harrington et al., 1999) and sable antelope (Chirima, 2010) populations in the nearby Kruger National Park, South Africa. In Hwange ecosystem, however, the lion *Panthera leo* population (i.e. the main predator for sable antelope), as well as populations of other large carnivores, decreased during the 1990s and at the beginning of the 2000s (Loveridge et al., 2007c). Sable antelope, moreover, only represents a small share in the diet of lion (Loveridge et al., 2007a) and hyaena *Crocuta crocuta* (Drouet-Hoguet, 2007). Predation has thus unlikely played a determinant role in trends of sable antelope densities across Hwange ecosystem during the 1990s.

We believe that elephant densities may explain the unexpected increase of sable antelope densities along the gradient of human disturbance in Hwange ecosystem. Chamaillé-Jammes et al. (2008) previously highlighted that the elephant population of Hwange National Park drastically increased from 15,000 to 35,000 individuals after the cessation of culling in 1986. The population, however, stabilized after 1992, which could probably explain why we failed to detect any temporal trend in elephant densities during the 1990s. Whether elephant populations in surrounding areas of the Park experienced a comparable increase is questionable. Elephants tend to avoid human-disturbed areas (van Aarde et al., 1999; Caro, 1999c; Hoare et du Toit, 1999). Thus, trophy hunting, human settlements, and livestock have most likely slowed down the increase of elephant populations outside Hwange National Park. Chamaillé-Jammes et al. (2008) even suggested that some elephants emigrated from the surrounding areas into the Park once culling was stopped. This probably exacerbated the difference of elephant densities between the Park and its periphery. As a result, sable antelope have constantly been exposed to much higher elephant densities, i.e. two to ten times, in the Park than in the surrounding areas throughout the 1990s. Under a scenario of asymmetric competition, this would not only explain the lower densities of sable in Hwange National Park, but also their decline observed only in the Park.

Valeix et al. (2007a) previously showed that sable antelope in Hwange National Park, and other medium-sized ungulates (i.e. impala *Aepyceros melampus*, greater kudu *Tragelaphus strepsiceros*, and roan antelope), were likely to suffer from costly interference from elephants at waterholes. With the elephant increase, these species shifted their temporal access to waterholes from late afternoon to midday in order to avoid high temporal overlap with elephants, and to limit interference competition (Valeix et al., 2007a). However, there is no measured evidence of a major direct cost to these adjustments (Valeix et al., 2009c), even though the increase in drought frequency in recent years (Chamaillé-Jammes et al., 2007) likely induced an increase in the constraint of surface water.

A reduction of wooded habitats due to higher densities of elephants in Hwange National Park could also explain lower densities of sable antelope compared to Matetsi Safari Area and Forestry/Gwaii Area, as well as their decline in the Park. We found no difference in percentages of wooded habitats, however, between Hwange National Park and its periphery. Similarly, Valeix et al. (2007c) observed no changes of vegetation structure at the landscape scale associated with elephant increases in Hwange National Park. Whether changes in vegetation structure due to elephant increase operated at a finer scale deserves further investigation. For instance, the availability of wooded habitats may have remained unchanged while their arrangement within the savanna may have detrimentally changed for sable antelope. Elephants aggregate around waterholes in the dry season, which creates a gradient of vegetation utilization that decreases with distance to water (Van Rooyen et al., 1994; de Beer et al., 2006). Woodland grazers, such as sable antelope, do not forage in the vicinity of waterholes. They regularly have to travel between waterholes and their feeding sites in woodlands (Redfern et al., 2003; Rahimi et Owen-Smith, 2007). With the elephant increase, the zone of impacted vegetation around waterholes may have extended (but see Chamaillé-Jammes et al., 2009), and so the distances between waterholes and feeding sites of sable also increased. Likewise, as we only focused on the tree layer, we may have overlooked possible changes of other vegetation components. Parker et al. (2009) showed in Ado National Park in South Africa, for instance, that higher elephant densities altered grasslands, with possible negative impacts on grazers like sable antelope.

The diversity of land uses across Hwange ecosystem might have played an unexpected role in sable antelope trends for the past decades. By slowing down the increase of the elephant population that followed the cessation of culling in 1986, human disturbance in the peripheral areas of Hwange National Park could have created a refuge for less competitive species, such as sable antelope, releasing some of the elephant impact on resources (i.e. change of vegetation, access to surface water). The role of elephant in African savannas is, however, still largely debated (Cumming, 1982; Fritz et al., 2002b; Skarpe et al., 2004) and further research is needed to propose a comprehensive mechanism about the impact of elephant on other large herbivores.

Conclusion

Hwange ecosystem presents an unconventional situation where the conservation status of a rare species, the sable antelope, is more secure in the surrounding areas of the National

Park than in the National Park itself. This challenges the widespread idea that National Parks alone can guarantee the conservation of wild species, and stresses the crucial importance of partially protected areas in their periphery in a context of human expansion over protected areas, and land use changes.

With the post-2000 drastic land ‘reform’ measures in Zimbabwe, land use changed in the surroundings of Hwange National Park and human encroachment increased, more particularly in the Forestry Area and in Gwaii ICA. The hunting concessions have been fragmented, and their leased reduced. This eventually risks jeopardizing the willingness of operators to invest in anti-poaching, wildlife management or community relations (e.g. in Cameroon, Mayaka et al., 2004). As a consequence, hunting industry has virtually collapsed in these areas (Bond et al., 2004; Lindsey et al., 2008), which has probably accentuated the decline of local incentives towards wildlife conservation, to the detriment of agriculture and logging. Poaching has particularly increased in the past years (Animal Life Line for Anti-poaching, Unpublished data). This may seriously compromise the future of sable antelope in Hwange ecosystem, one of the major conservation pockets for this species.

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CHAPITRE 7

DISCUSSION GÉNÉRALE

WILLIAM CROSMARY

Ce travail de thèse s'inscrit dans la prise de conscience progressive que la conservation de la faune et des habitats naturels peut, et doit, s'étendre à l'extérieur des aires strictement protégées que sont les parcs nationaux (catégories I-III UICN *sensu* WRI/UNEP/UNDP/WB, 1996; Fjeldsa et al., 2004; Newmark, 2008; Western et al., 2009). Les zones de chasse touristique par exemple, où la chasse aux trophées est pratiquée, s'avèrent être des zones de conservation potentiellement pertinentes (Dickson et al., 2009). D'une part, la manne financière qu'elles représentent peut être une alternative économique viable à d'autres activités humaines beaucoup plus néfastes pour les habitats naturels, e.g. agriculture commerciale ou élevage intensif. D'autre part, une partie de l'argent qu'elles génèrent peut être redistribuée dans la gestion et la conservation des habitats naturels et des populations animales que ces zones abritent (e.g. Lewis et Alpert, 1997; Leader-Williams et al., 2001; Lindsey et al., 2006), ce que les gouvernements de pays en développement peinent parfois à faire pour leurs parcs nationaux (Leader-Williams et Albon, 1988).

La base d'une gestion éclairée des populations animales, et à fortiori des populations exploitées, requiert l'utilisation de suivis à long terme renseignant, entre autres, sur la dynamique de ces populations et leurs tendances démographiques (Caughley et Gunn, 1995; Buckland et al., 2000). Mais rares sont de telles études en dehors des parcs nationaux, et encore plus rares sont les études qui comparent les populations de zones exploitées à celles de zones non exploitées. Sans ces suivis et ces comparaisons, il n'est pas possible de statuer sur le potentiel de conservation de ces zones de chasse.

En plus des suivis populationnels, dynamiques et démographiques, l'étude comportementale est un autre outil proposé en biologie de la conservation pour évaluer l'effet des perturbations anthropiques sur les populations animales (Sutherland, 1998; Caro, 2007). L'ampleur des changements comportementaux, comme l'augmentation du temps que les individus passent en vigilance ou les changements du patron temporel d'activités, devrait en effet renseigner sur l'intensité de la perturbation subie (e.g. Carney et Sydeman, 1999).

Sans le recours à des suivis populationnels à long terme, ainsi qu'aux observations comportementales dans les zones de chasse, on risque de ne pas détecter les effets de la chasse aux trophées autres que le simple prélèvement d'un certain nombre d'animaux dans les populations chassées, e.g. proportion diminuée de mâles adultes, taille de cornes en déclin, changements comportementaux (e.g. Coltman et al., 2003; Milner et al., 2007). *In fine*, l'utilisation de suivis populationnels et d'études comportementales devrait faciliter la gestion adaptative de ces zones de chasse, et la décision d'ajuster ou non la perturbation, e.g. les quotas de chasse.

Dans ce contexte, l'objectif de ce travail de thèse était double. Sur le plan **scientifique** d'une part, il s'agissait d'évaluer les effets subtiles – peu étudiés – de la chasse aux trophées sur les grands herbivores: i) sur le comportement à l'échelle individuelle et à l'échelle des groupes, ii) sur la proportion de mâles adultes, la taille des cornes, et les densités à l'échelle des populations. Sur le plan de la **gestion** et de la **conservation** d'autre part, il s'agissait de définir, dans un contexte de réforme foncière et de changement d'utilisation des terres, ainsi que de difficultés économiques, si les zones de chasse réussissaient à tenir leur rôle de conservation des populations de grands herbivores. Enfin, pour nos partenaires au Zimbabwe, l'autorité gouvernementale de la gestion de la faune (i.e. *Zimbabwe Parks and Wildlife Management Authority*), et les gestionnaires des zones de chasse (i.e. *Gwaii Intensive Conservation Area*, *Matetsi Safari Area*), il s'agissait aussi de dresser un état des lieux après 30 années de chasse touristique.

Pour se faire, nous avons utilisé des données d'observations comportementales effectuées sur le terrain au cours de cette thèse, et avons eu recours à des archives historiques de données populationnelles issues de suivis à long terme. Nous avons opté pour une approche multi spécifique afin de vérifier si l'écologie de chacune des espèces, et leur attrait cynégétique, pouvaient influencer leur réponse comportementale au risque de chasse, ainsi que leur réponse populationnelle au prélèvement (i.e. proportion de mâles adultes, taille de cornes, densités de population). Autant que possible, cette thèse a comparé les comportements des grands herbivores africains, et leur trajectoire populationnelle, entre le Parc National de Hwange, Zimbabwe, et les zones de chasse aux trophées adjacentes.

LES EFFETS INDIRECTS DE LA CHASSE AUX TROPHÉES: AJUSTEMENTS COMPORTEMENTAUX EN RÉPONSE AU RISQUE DE CHASSE

La chasse aux trophées induit des ajustements comportementaux

Nos travaux illustrent comment les populations d'herbivores chassées sont susceptibles de déplacer leur patron temporel d'activités pour diminuer leur recouvrement avec les périodes de chasse (***Chapitre 2***). C'est ce que l'on a observé dans les périodes de visites aux points d'eau des trois espèces à l'étude dans cette partie de la thèse, l'impala, le grand koudou, et l'hippotrague noir. Ce sont trois espèces dépendantes de l'eau de surface (Bothma et al., 2002) qui viennent d'ordinaire (i.e. sans chasse) s'abreuver aux points d'eau presque exclusivement pendant le jour (***Chapitre 2***; Weir et Davison, 1965; Ayeni, 1975; Valeix et al., 2007a). Dans les zones de chasse, néanmoins, la fréquence des visites nocturnes aux points d'eau augmente. Ce déplacement de la niche des proies le long de l'axe temporel est rapporté dans quelques études prédateurs-proies (revue dans Kronfeld-Schor et Dayan, 2003; Caro, 2005). Et les activités anthropiques, la chasse en particulier, peuvent comme les prédateurs naturels inciter les proies à changer des activités habituellement diurnes à la nuit (Madsen et Fox, 1995; Kitchen et al., 2000). Plus rares néanmoins sont les études comme la nôtre, qui ont documenté des ajustements temporelles de la niche pour des proies exposées à la fois au risque de prédation naturelle, et au risque de chasse (mais voir Kilgo et al., 1998). Nos résultats montrent que les groupes d'herbivores des zones de chasse renoncent à venir au point d'eau et retournent dans le couvert protecteur de la végétation plus souvent que les groupes du parc national (***Chapitre 3***). De plus, dans les groupes qui décident tout de même de s'approcher des points d'eau pour venir boire, les individus sont en général plus vigilants que ceux des groupes du parc national.

Ces observations comportementales ont été effectuées sans stimulation volontaire de notre part. Durant nos observations, nous étions silencieusement postés à distance des points d'eau (typiquement >100m), et cachés dans des filets de camouflage, dans la végétation, ou encore sur des plateformes d'observation. Nous avons de ce fait limité les stimuli induits sonores et visuels. Les ajustements comportementaux observés illustrent par conséquent davantage une réponse durable à un dérangement chronique plutôt qu'une réponse passagère à un dérangement induit, e.g. la fuite face à un chasseur/prédateur qui avance (revue dans Stankowich, 2008). Nous ne pouvons cependant pas écarter la possibilité que les animaux aient pu repérer notre présence en nous sentant lors des observations comportementales. Néanmoins, si cela avait été le cas, il est probable que la réponse comportementale adoptée eût été la fuite. En effet, lorsque la présence de l’humain est détectée (i.e. stimulus visuel induit), les animaux des zones de chasse fuient immédiatement (Tarakini et al., données non publiées). Or ceci n’est arrivé qu’en de rares occasions lors de nos observations, notamment lorsque le vent tournait et que nous nous trouvions alors sous le vent. Nos travaux montrent toutefois qu’il y a des ajustements comportements qui s’expriment aux échelles des groupes et des individus. Que le risque de chasse soit chronique ou bien fréquemment induit, nous montrons qu’il y a pour les grands herbivores des zones de chasse l’obligation d’ajuster durablement et/ou fréquemment leurs comportements.

Mais quelle(s) différence(s) cela fait-il? S’agit-il d’ajustements coûteux?

Les grands herbivores africains ajustent leur comportement au risque de chasse, en particulier lors de l’acquisition de l’eau de surface. Ce qui demeure méconnu, par contre, et quelles sont les conséquences de ces ajustements pour la population. De constater que la chasse aux trophées perturbe les comportements n’a d’importance que si les ajustements comportementaux effectués en réponse au risque de chasse affectent réellement les animaux des zones de chasse, ainsi que leur population. Par exemple, en contrariant leurs activités usuelles telles que l’acquisition des ressources, la recherche de partenaires sexuels, les soins parentaux, le repos, etc. Et que ceci se traduise en un déclin de la valeur adaptative des individus, i.e. survie et reproduction diminuées, et se répercute à l’échelle de la population provoquant la chute des effectifs.

Ce travail de thèse ne mesure pas ces coûts potentiels associés aux ajustements comportementaux. Il ne nous est donc pas possible à ce stade de dire si le changement de patron temporel des visites aux points d’eau, ou la plus grande vigilance, affectent véritablement les individus, et *in fine* leur population. A notre connaissance, le lien entre les ajustements comportementaux en réponse au risque de chasse, la valeur adaptative individuelle, et la dynamique des populations n’a jamais été clairement montré. Il existe en revanche une vaste littérature à ce sujet dans le cadre des relations prédateurs-proies. Le risque de prédation conditionne le temps et l'énergie que les proies peuvent allouer à l'alimentation, ou à la reproduction (Lima et Dill, 1990; Lima, 1998b). L'animal doit faire un compromis entre le risque lié à la prédation et les bénéfices découlant de l'acquisition des ressources, ou de la rencontre du partenaire sexuel (revue dans Lima, 1998a). Or, l'investissement dans des comportements d'anti-prédation se fait souvent au détriment de l'alimentation, ou des opportunités d'appariement (Lima et Dill, 1990; Lima, 1998a). Ces effets non-léthaux du risque de prédation[15] (sensu Lima, 1998a) risquent donc à moyen et long terme d'altérer la valeur adaptative des individus, la dynamique de leur population (Creel et al., 2007; Creel et Christianson, 2008), et la structure et le fonctionnement des écosystèmes (Brown et al., 1999; Ripple et Beschta, 2004). De la même manière, on peut penser que les ajustements comportementaux en réponse au risque de chasse peuvent altérer la valeur adaptative des individus, et éventuellement la dynamique des populations chassées.

Les ***Chapitres 2*** et ***3*** montrent que les ajustements comportementaux en réponse au risque de chasse contrarient l'acquisition de l'eau de surface, ressource clef pour les grands herbivores des savanes semi-arides africaines (Western, 1975; Thrash et al., 1995; Owen-Smith, 1996). La plupart des grands herbivores d'Afrique ont en effet des besoins quasi journaliers en eau (Bothma et al., 2002), particulièrement lors des périodes les plus sèches (Valeix et al., 2007b). Dès lors, se pose la question des conséquences pour les herbivores qui renoncent à boire à cause du risque de chasse.

La température ambiante élevée et les radiations solaires sont sources de stress physiologique chez les animaux des savanes semi-arides. Pour de nombreuses espèces, boire est vital pour abaisser la température corporelle et remplacer l'eau perdue par l'organisme lors de la transpiration (Taylor, 1970; Mitchell et Laburn, 1985). Ce besoin de thermorégulation conditionne les comportements quotidiens, et peut donc restreindre le temps qui peut être alloué à la recherche de nourriture (e.g. Owen-Smith, 1998 ; Brain et Mitchell, 1999; Maloney et al., 2005). Ainsi, la température corporelle d'un animal qui manque une opportunité de s'abreuver risque d'augmenter et son taux d'activité de diminuer. De plus, l'animal risque de devoir attendre dans les environs du point d'eau le

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[15] De l'anglais « *non-lethal effects* ».

moment opportun (i.e. moins de risque de chasse) pour s'approcher de l'eau et boire. En plus d'augmenter le stress physiologique de l'animal, renoncer à boire peut se répercuter sur son budget d'activité. D'une part justement parce que le besoin de thermorégulation restreint les activités, mais aussi parce que les sites d'alimentation en saison sèche sont généralement éloignés des points d'eau pour les brouteurs (grand koudou, impala en saison sèche) et les paisseurs sélectifs (hippotrague noir) (Redfern et al., 2003; Rahimi et Owen-Smith, 2007). Enfin, l'animal qui reste dans les environs du point d'eau en attendant de pouvoir venir y boire risque davantage de rencontrer ses prédateurs naturels. En effet, les zones de points d'eau sont des zones dangereuses pour les herbivores (Valeix et al. 2007b, 2009b).

Pour les herbivores qui décident de venir boire de nuit, ce risque est d'autant plus grand puisque leurs prédateurs sont essentiellement nocturnes et se présentent aux points d'eau la nuit pour boire et chasser leurs proies (***Chapitre 2***; Valeix et al., 2009b). Cette bascule des activités à la nuit en réponse au risque de chasse qui engendre une exposition accrue aux prédateurs naturels a été évoquée dans d'autres écosystèmes. Kilgo et al. (1998) suggèrent ainsi qu'en augmentant ses activités nocturnes à cause du risque cynégétique diurne, le cerf de Virginie (*Odocoileus virginianus*) s'expose davantage à la prédation de la panthère de Floride (*Felis concolor coryi*).

La vigilance individuelle augmente autour des points d'eau en réponse au risque de chasse pendant les phases d'approche et de départ, et ce au détriment de la marche (***Chapitre 3***). Par conséquent, le temps passé dans les zones ouvertes autour des points d'eau, et donc le temps d'exposition aux radiations solaires (i.e. stress de thermorégulation), et aux prédateurs naturels, s'en trouve allongé. Bien qu'étant composés d'individus plus vigilants, et donc plus lents à se déplacer, les groupes d'herbivores des zones de chasse ne passent pas plus de temps dans les zones de points d'eau que les groupes du parc national. Ceci suggère une plus grande synchronie et cohésion entre les individus des groupes dans les zones de chasse (***Chapitre 3***). Les individus peuvent bénéficier de la cohésion de leur groupe du fait de la diminution du risque de prédation *per capita* (Hamilton, 1971; Pulliam, 1973; Lingle, 2003). Mais il peut aussi leur falloir en payer les coûts s'il leur faut compromettre leurs propres besoins/activités pour suivre les autres membres du groupe (e.g. Côté et al., 1997; revue dans Conradt et Roper, 2005).

Ainsi, même si ce travail de thèse ne permet pas de statuer définitivement sur l'existence ou non de coûts liés aux ajustements comportementaux des grands herbivores africains en réponse au risque de chasse, il semble très probable que ces ajustements ne soient pas sans conséquence sur la valeur adaptative des individus. Evidemment, la prochaine étape pour compléter ce travail sera d'essayer de mettre clairement en évidence le lien entre ces ajustements comportementaux et les coûts encourus par les individus. Ainsi, conviendrait-il par exemple de tester si le succès de chasse des prédateurs naturels en périphérie des points d'eau est supérieur dans les zones de chasse par rapport au parc national à cause de la bascule nocturne des visites des grands herbivores. On pourrait, d'autre part à l'aide de colliers GPS, suivre les mouvements des groupes d'herbivores après une opportunité de boisson manquée, pour voir si cela les contraint à rester de plus longues périodes à proximité des points d'eau, réduit le taux d'activité des individus, et compromet ainsi d'autres activités tel que l'alimentation.

Limites de l'approche comportementale comme révélateur de la perturbation anthropique

L'écologie comportementale doit voir son rôle prendre de l'importance dans la biologie de la conservation (Sutherland, 1998; Caro, 2007). Dans un monde inexorablement anthropisé, il y a une préoccupation grandissante de savoir si et comment la perturbation humaine affecte le comportement animal (Geist, 1970; Caro, 1999a; Barber et al., 2010). Le temps passé en vigilance et les distances de fuite ont ainsi été largement utilisés comme métriques comportementales indicatrices du degré de perturbation humaine (revues dans Frid et Dill, 2002; Stankowich, 2008). Mais ces indicateurs comportementaux ne reflètent pas toujours bien le degré de perturbation humaine subie par l'animal (Gill et al., 2001). Les animaux n'ont en effet pas toujours la possibilité de répondre à la perturbation en changeant leur comportement. La condition physique et physiologique des individus influence les décisions (McNamara et Houston, 1996), et les individus en plus mauvaise condition, ou ceux qui dépendent le plus des ressources, risquent d'être moins aptes à altérer leur comportement en réponse à la perturbation humaine (e.g. Beale et Monaghan, 2004).

Ainsi, les ***Chapitres 2*** et ***3*** illustrent comment les contraintes environnementales (i.e. besoin en eau et risque de prédation naturelle) restreignent l'amplitude des ajustements comportementaux possibles en réponse au risque de chasse. Alors que l'impala, le grand koudou et l'hippotrague noir de notre étude subissent en zones de chasse la même perturbation cynégétique, ces herbivores ne répondent pas pour autant avec la même amplitude au risque de chasse. Le grand koudou, plus vulnérable aux prédateurs naturels, est l'espèce moins encline à basculer ses visites aux points d'eau aux périodes nocturnes (***Chapitre 2***). De même, le grand koudou est l'espèce naturellement (i.e. dans le parc national) la plus vigilante. Périquet et al. (2010) ont d'ailleurs suggéré que le grand koudou était proche du maximum de vigilance dans le Parc National de Hwange, et que par conséquent, il ne devrait pas être capable d'augmenter de beaucoup son niveau de vigilance, même si le risque perçu augmentait. C'est ce que nous avons observé dans les zones de chasse où le grand koudou est l'espèce qui a augmenté le moins son niveau de vigilance en réponse au risque de chasse (***Chapitre 3***). Ces résultats montrent que l'espèce la plus exposée à la prédation naturelle n'est pas forcément celle qui répond le plus au risque de chasse (Beale et Monaghan, 2004). De même, l'espèce la plus contrainte par la ressource eau dans notre étude, l'hippotrague noir, n'a pas augmenté sa vigilance pendant la période d'abreuvement (***Chapitre 3***).

Ces résultats illustrent comment et pourquoi des animaux perturbés par le risque de chasse n'ajustent pas systématiquement leur comportement en conséquence. Dès lors, l'absence d'ajustement comportemental ne signifie pas forcement absence de dérangement, ou que les animaux en question sont peu sensibles au dérangement, ou encore qu'ils s'y sont habitués. Pour les études comportementales qui cherchent à identifier la perturbation humaine via des indices comportementaux, il s'agit donc de réaliser qu'en fonction de leur activité en cours, les animaux sont plus ou moins aptes à ajuster leur comportement à la perturbation, et que différentes espèces répondent différemment à une même perturbation en fonction de leurs contraintes écologiques. En ce sens, l'approche multi spécifique est la plus à même de renseigner sur les effets du dérangement anthropique sur un écosystème (Blumstein et al., 2005).

Plus généralement, nos résultats semblent aller dans le sens de l'hypothèse de l'allocation de risque[16] formulée par Lima et Bedkenoff (1999). Le risque de prédation

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[16] De l'anglais « *Risk-allocation hypothesis* ».

n’étant pas constant dans le temps, les animaux doivent répondre rapidement aux changements de risque et d’intensité du risque (Kats et Dill, 1998; Lima, 1998b). Les proies doivent donc résoudre le problème de comment, et quand, le mieux (i.e. de façon optimale) allouer les efforts à l’acquisition des ressources et aux comportements d’anti-prédation sous différents états de risque. Si les périodes de haut risque sont brèves ou rares, alors, au cours d’une de ces périodes, la proie peut suspendre son approvisionnement au profit d’un comportement d’anti-prédation, et éventuellement reprendre sa séquence d’approvisionnement lorsque le risque décroît. En revanche, si les périodes de haut risque sont longues et/ou fréquentes, la proie n’a pas d’autre choix que de continuer de s’approvisionner en période de haut risque. Donc, selon cette hypothèse, les proies exposées de manière chronique à un haut risque, e.g. prédation et chasse, devraient recourir à des comportements d’anti-prédation plus modérés, et peut-être moins prévisibles (Scannel et al., 2001) que ceux auxquels on pourrait s’attendre.

Quelques perspectives de recherche et de gestion

Les approches comportementales ne sont donc pas toujours suffisantes pour évaluer la perturbation anthropique que subissent les animaux. De plus en plus, l’approche physiologique vient compléter les études comportementales. Cette approche, autrement qualifiée de physiologie de la conservation (revue dans Wikelski et Cooke, 2006), permet de révéler les effets physiologiques du dérangement anthropique (e.g. sécrétion de glucocorticoïdes, dépenses énergétiques) lorsque que les effets sur le comportement ne sont parfois pas détectés (e.g. Walker et al. 2005, 2006).

L’utilisation complémentaire de l’écologie comportementale et de la physiologie est donc souhaitable dans l’étude et l’évaluation des effets indirects de la perturbation anthropique sur les animaux. Cette double approche semble en effet être la plus à même de révéler les mécanismes – comportementaux et physiologiques – induits par la perturbation humaine, qui peuvent se traduire en une survie et/ou reproduction individuelles diminuées. A l’échelle de la population, il conviendrait alors de tenir compte de ces effets indirects dans les modèles de dynamique des populations perturbées ou exploitées (Sutherland, 1996).

La problématique des grands herbivores qui doivent faire face à la fois au risque de prédation naturelle et au risque de chasse ne concerne pas que les savanes africaines. Elle s'étend aux écosystèmes de l'hémisphère Nord où de nombreuses populations de grands herbivores sont exploitées, et voient petit à petit le retour de leurs prédateurs naturels. Dans ces écosystèmes où les grands carnivores font leur retour après des siècles de persécution humaine (Berger, 1999; Andersen et al., 2006), la façon dont leurs proies vont réagir et intégrer ce double risque prédateurs/chasseurs dans leur comportement risque d'être une question brûlante dans les années à venir.

LES EFFETS DIRECTS DE LA CHASSE AUX TROPHÉES: LONGUEUR DE CORNES, PROPORTION DE MÂLES ADULTES, ET DENSITÉS DE POPULATION

Des cornes pas forcément plus courtes au fil des années

Trente années de chasse aux trophées dans les zones de chasse de la *Matetsi Safari Area,* Zimbabwe, n'ont pas conduit à un déclin de la longueur des cornes chez l'impala, le grand koudou, ou l'hippotrague noir, aussi spectaculaire que celui observé chez le mouflon américain (*Ovis canadensis*) de *Ram Mountain* au Canada (Coltman et al., 2003), ou chez le mouflon méditerranéen (*Ovis gmelini musimon* × *Ovis sp.*) du Massif de Caroux-Espinouse en France (Garel et al., 2007). Les mâles de la population de mouflon de *Ram Mountain* ont en effet connu un déclin de ca. 30% de la longueur de leurs cornes depuis 30 ans, et celles du mouflon de Caroux-Espinouse un déclin de ca. 12% depuis 20 ans. C'est deux à huit fois plus que ce que nous avons observé chez l'hippotrague noir (i.e. diminution de 6%) et chez l'impala (i.e. diminution de 4%), et évidemment sans commune mesure avec le grand koudou pour lequel la longueur des cornes a augmenté (i.e. augmentation de 14%) au cours des 30 dernières années (***Chapitre 4***). Pourquoi une telle différence entre les mouflons et les herbivores africains?

Un premier élément de réponse vient du taux de prélèvement des mâles adultes dans ces populations chassées. Il apparaît que l'espèce qui a subi en moyenne le taux de prélèvement de mâles le plus élevé, i.e. l'hippotrague noir, est celle pour laquelle le déclin de la longueur des cornes est le plus prononcé (***Chapitre 4***). Chez le grand koudou en revanche, le taux de prélèvement des mâles a diminué au fil des années, et c'est la seule espèce des trois pour laquelle la longueur des cornes a augmenté. Les taux de prélèvements subis par les espèces à l'étude, i.e. en moyenne 5.4%, 7.7%, et 12% par an respectivement pour impala, grand koudou, et hippotrague noir, sont bien moindres que les taux de prélèvements pratiqués chez les populations de grands herbivores de l'hémisphère Nord, e.g. au moins 40% des béliers chassables en moyenne par année à *Ram Mountain* (Coltman et al., 2003), et 20% à Caroux-Espinouse (M. Garel communication personnelle). C'est donc que les exemples de déclin de la longueur des cornes chez les grands herbivores concernent des populations qui ont été exploitées à des taux généralement supérieurs à ceux que nous avons observés (***Chapitre 4)***.

Pour l'impala, le raccourcissement des cornes résulte d'une diminution de l'âge moyen des mâles prélevés. Ce qui semble indiquer que l'âge moyen des mâles dans la population d'impala a diminué au fil des années. La diminution de l'âge moyen des mâles dans les populations de grands herbivores chassées pour les trophées a été illustrée dans plusieurs études (Laurian et al., 2000; Stubsjøen et al., 2000; Sæther et al., 2004). Le rajeunissement des mâles dans la population peut avoir des répercussions sur les comportements reproducteurs (e.g. Noyes et al., 1996; Singer et Zeigenfuss, 2002; Holand et al., 2006), et donc éventuellement sur le recrutement et la dynamique de population (Larkin et al., 2002; Noyes et al., 2002; Holand et al., 2003; Sæther et al., 2003). La diminution de la taille des cornes, par contre, ne devrait pas être irréversible puisqu'il est le résultat de la diminution de l'âge moyen des mâles. Pour inverser la tendance, il devrait suffire de diminuer le taux de prélèvement effectué sur les mâles de façon à augmenter les chances de ces derniers de vivre plus vieux. L'exemple du grand koudou indique en effet qu'à mesure que le taux de prélèvement a diminué au fil des ans, l'âge des mâles récoltés a augmenté, ainsi que la longueur de leurs cornes. Pour l'hippotrague noir, le problème de la diminution de la taille des cornes est probablement plus sérieux puisqu'il est indépendant de l'âge des mâles récoltés, et pourrait donc avoir des bases génétiques. Si tel est le cas, il ne sera peut-être pas possible d'inverser ce déclin de longueur des cornes chez cette espèce. Conover et al. (2009) ont montré que le déclin de la taille et de la masse corporelles des poissons dans les populations pêchées, pouvait être inversé dans un laps de temps de quatre générations en changeant le mode de prélèvement, i.e. en pêchant surtout les poissons plus petits et en laissant survivre les plus gros. Est-ce réalisable sur des espèces plus grosses, aux temps de génération plus longs, comme les grands herbivores? Il semble que oui. Jachmann et al. (1995) ont observé chez la population d'éléphants (*Loxodonta africana*) du sud du Parc National de Luangwa, Zambie, que la proportion d'individus sans défense avait diminué de 40% à 20% dans les années 1990 après deux décades de braconnage. Ceci notamment grâce à la mise en place d'une régulation stricte du commerce international de l'ivoire, ainsi qu'à l'immigration d'éléphants depuis des zones non/moins braconnées. Inverser, ou tout du moins ralentir, la diminution de la taille d'un trait physique est donc aussi possible chez les grands herbivores. Dès lors la question est de savoir à quelles fins. Et là deux critères interviennent, biologique et économique.

Sur le plan biologique, une plus petite taille des cornes et un déclin de la masse corporelle réduisent la valeur reproductive des mâles (Cotlman et al., 2003), et peuvent donc altérer la dynamique des populations exploitées. Nos résultats ne permettent pas de dire si le raccourcissement de 6% de longueur des cornes chez l'hippotrague noir a eu un impact négatif sur la valeur reproductive des mâles de la population. Pour le tester, il faudrait recourir à des analyses de génétique quantitative comparables à celles de Coltman et al. (2003). À l'échelle de la population, on remarque tout de même que la densité d'hippotragues noirs dans les zones de chasse de Matetsi a chuté de ca. 35% au cours des même 30 dernières années (***Chapitre 4***). Durant la même période, la densité d'hippotragues noirs du Parc National de Hwange a chuté autant, voire davantage (***Chapitres 5*** et ***6***). L'effet de la chasse aux trophées sur la dynamique de population, par le truchement d'un déclin de la valeur reproductive des mâles, n'est probablement pas le principal responsable du déclin observé de la population d'hippotragues noirs dans les zones de chasse. En effet, le déclin concomitant de cette espèce dans les zones sud de Matetsi et dans le Parc National de Hwange suggère que d'autres facteurs ont été en jeu, e.g. récurrence des sècheresses, prédateurs naturels, éléphant (***Chapitre 5***).

Sur le plan économique ensuite, il appartient aux gestionnaires de décider si un déclin de quatre et six pourcents chez l'impala et l'hippotrague noir risque de compromettre l'attractivité de leurs zones de chasse. Dans ce commerce compétitif, la perspective de pouvoir prélever des trophées de haute qualité, i.e. mâles aux plus grandes cornes, peut guider les clients chasseurs dans leur choix de destination cynégétique. A notre connaissance, il n'y a pas d'étude qui montre explicitement le lien entre un déclin de la taille des cornes dans une zone de chasse et la performance économique de la zone en question. En Amérique du Nord et en Europe cependant, ce lien paraît évident lorsque les plus gros mâles sont mis aux enchères, ou que les taxes de chasse augmentent à postériori avec la longueur des cornes des animaux prélevés (Festa-Bianchet, 2003; Garel et al., 2007). De la présence de gros trophées dans une zone de chasse ne dépend pas uniquement la performance économique de la zone, mais aussi sa performance de conservation. Tant que la zone est économiquement compétitive, elle peut représenter une alternative commerciale à d'autres activités anthropiques autrement plus destructrices pour les habitats naturels comme l'agriculture commerciale et l'élevage extensif (mais voir en Afrique de l'Ouest; UICN/PACO, 2009).

Les enjeux d'une gestion éclairée de la longueur des cornes chez les grands herbivores africains dans les zones de chasse sont multiples, i.e. biologique, économique, et de conservation. Aux taux de prélèvement de mâles effectués dans la zone de chasse de Matetsi Safari Area, i.e. environ 10% par année, l'effet sur les variations de la longueur des cornes est assez minime (***Chapitre 4***). La situation des espèces les plus prisées, telles que l'hippotrague noir, est néanmoins préoccupante parce que les résultats suggèrent que le raccourcissement des cornes chez cette espèce pourrait avoir des bases génétiques, et parce que le Parc National de Hwange s'avère être une source potentielle d'individus très limitée pour les zones de chasse de la *Matetsi Safari Area*.

Un autre intérêt de l'approche multi spécifique, non exploité dans cette thèse, est de voir si la sélection sexuelle peut influencer les tendances temporelles de la taille des cornes, en contrebalançant l'effet sélectif de la chasse aux trophées. La sélection sexuelle favorise le développement de grandes cornes chez les grands ongulés, plus particulièrement chez les espèces polygynes (Caro et al., 2003). Cette sélection sexuelle semble être plus intense chez les espèces formant de grands groupes, et pour lesquelles les mâles sont moins territoriaux (Bro-Jørgensen, 2007). On pourrait donc s'attendre à ce que le déclin de la taille des cornes, à taux de prélèvements égaux, soit moins marqué chez ces espèces.

Zones de chasse et potentiel de conservation des grands herbivores africains

L'écosystème de Hwange est représentatif de la diversité des types d'utilisation des terres en Afrique, i.e. une mosaïque d'aires protégées, partiellement protégées, et ouvertes, sur des terres d'état, privées ou communales le long d'un gradient de perturbation humaine (Peace Parks Foundation, 2009). Que nous apprend cet écosystème sur le potentiel de conservation des grands herbivores dans les zones de chasse en Afrique, et en particulier sur leur capacité à maintenir des densités de populations comparables aux zones strictement protégées que sont les parcs nationaux? Malgré le prélèvement, les ajustements comportementaux en réponse au risque de chasse (***Chapitres 2*** et ***3***), le raccourcissement des cornes chez certaines espèces (***Chapitre 4***), ou la tendance les plus faibles proportions de mâles adultes dans certaines populations (***Chapitre 5***), le complexe de chasse de Matetsi abrite aujourd'hui des densités de populations d'herbivores aussi élevées, voire plus élevées, que le Parc National de Hwange (***Chapitres 5*** et ***6***).

Au cours des trois dernières décennies, les populations de grands herbivores ont globalement décliné à Matetsi et dans le Parc National de Hwange. Les précipitations, en particulier pendant la saison sèche, déterminent fortement les abondances des grands herbivores dans les savanes semi-arides africaines (Owen-Smith, 1990; Fritz et Duncan, 1994; Mduma et al., 1999). L'écosystème de Hwange, à l'instar du reste de l'Afrique australe, a connu une recrudescence d'épisodes de sécheresse dans les années 1990 (Hulme et al., 2001; Nicholson, 2001; Chamaillé-Jammes et al., 2006), en partie responsable du déclin de nombreuses populations de grands herbivores (e.g. Mduma et al., 1998; Ottichilo et al., 2001; Dunham et al., 2003, 2004). Il semble que la récurrence des sécheresses dans la décennie 1990 ait été la principale responsable du déclin général des grands herbivores dans l'écosystème de Hwange aussi (***Chapitre 5***). En effet, ce déclin a particulièrement touché les paisseurs sélectifs, i.e. cobe des roseaux (*Redunca arundinum*), hippotrague noir, phacochère (*Phacochoerus aethiopicus*) et cobe à croissant (*Kobus ellipsiprymnus*). Or, ces derniers sont davantage vulnérables aux sécheresses que les brouteurs (i.e. girafe [*Giraffa camelopardalis*], grand koudou), les herbivores au régime alimentaire mixte (i.e. éléphant, impala), et les paisseurs non sélectifs (i.e. buffle [*Syncerus caffer*], zèbre [*Equus burchelli*]) (Owen-Smith, 2008). Pour la plupart néanmoins, le déclin a été moins marqué dans les zones de chasse que dans le parc national. Pour certaines, les densités dans les zones de chasse de Matetsi ont même augmenté, alors qu’elles ont au cours de la même période diminué dans le parc national (***Chapitre 5***). En termes de conservation des grands herbivores, le complexe de chasse de Matetsi a donc joué, et joue encore aujourd’hui, un rôle déterminant dans l’écosystème de Hwange. Comment expliquer le constat peu commun que des zones de chasse semblent mieux réussir qu’un parc national à protéger les populations de grands herbivores (mais voir Caro, 1999b; Setsaas et al., 2007; Stoner et al., 2007)? C’est qu’il y a très certainement d’autres facteurs que la chasse à prendre en compte dans le système.

Le rôle de la prédation comme mécanisme de régulation des populations d’herbivores est de plus en plus reconnu dans les savanes africaines (Grange et al., 2004; Owen-Smith et Mills, 2006), notamment pour les herbivores de masse inférieure à 150kg (Sinclair et al., 2003; Fritz et al., 2011). Les données historiques sur les grands carnivores sont habituellement rares, et l’écosystème de Hwange ne fait pas exception à la règle. Il n’est donc pas aisé de discuter de l’effet qu’a pu avoir ce facteur sur les populations de grands herbivores au cours des 30 dernières années. Il est néanmoins probable que le facteur prédation ait été l’un des artisans des trajectoires contrastées des densités d’herbivores entre Matetsi et le Parc National de Hwange. Entre 1971 et la première moitié des années 1990, le nombre de lion, léopard, et hyène tachetée a en effet doublé dans le Parc National de Hwange (Wilson, 1997). Cette augmentation des populations de grands carnivores a probablement été facilitée par la profusion de carcasses d’éléphant générées par les opérations d’abattage dans le parc national jusqu’en 1986 (Cumming, 1981). Et ce, plus particulièrement pour les deux principaux prédateurs du système, lion et hyène, dont une partie du régime alimentaire est composée de charognes (Drouet-Hoguet, 2007; Loveridge, 2007b). Nous ne disposons pas d’information historique sur les abondances des prédateurs à Matetsi. Nous pouvons tout de même supposer qu’elles ont été moindres que dans le parc national du fait du prélèvement (i.e. 8% chez les grands carnivores; Cumming, 1989), et du dérangement occasionné par la chasse. C’est notamment plausible pour le lion et le léopard dont les populations sont particulièrement affectées par le prélèvement des mâles adultes (Packer et Pusey, 1984; Greene et al., 1998; Loveridge et al., 2007a). Après l’arrêt de l’abattage des éléphants en 1986 dans le Parc National de Hwange, la disponibilité en carcasses d’éléphant a dû diminuer. Les prédateurs, hyène et lion en particulier, ont alors probablement eu à basculer leur régime alimentaire vers les autres espèces d'herbivores. Cela pourrait expliquer pourquoi les densités des espèces d'herbivores ont généralement davantage diminué dans le Parc National de Hwange que dans le complexe de chasse de Matetsi (***Chapitre 5***). Les estimations récentes montrent néanmoins que les abondances de ces prédateurs sont aujourd'hui équivalentes entre le parc national et Matetsi (Elliot, 2007), et ce probablement grâce à la réduction des taux de prélèvement ainsi qu'au moratoire sur la chasse au lion mis en place en 2003. Par conséquent, si la prédation naturelle a été, et est encore aujourd'hui, un facteur déterminant de la dynamique des populations de grands herbivores dans le système, nous devrions assister à un déclin de ces populations au cours des prochaines années dans le complexe de chasse de Matetsi.

L'éléphant est un autre facteur biotique qui a peut-être joué un rôle prépondérant dans notre aire d'étude. C'est la seule espèce de grand herbivore dont la population a augmenté au cours des 30 dernières années, à la fois dans le Parc National de Hwange, et dans une moindre mesure dans le complexe de chasse de Matetsi (***Chapitres 5*** et ***6***). La population d'éléphants de l'écosystème Hwange a bénéficié de l'arrêt de l'abattage systématique, passant de moins de 20,000 individus dans la période pré-1986 à ca. 30,000 aujourd'hui dans le parc national (Chamaillé-Jammes et al., 2008). Le rôle de l'éléphant sur le fonctionnement des savanes d'Afrique, et sur les populations des autres grands herbivores, suscite beaucoup de passion et de débat depuis les 30 dernières années (e.g. Cumming, 1982; Cumming et al., 1997; Skarpe et al., 2004; O'Connor et al., 2007; Valeix et al., 2007a, 2009c; Guldemond et van Aarde, 2008). Le ***Chapitre 6*** suggère que les hippotragues noirs se maintiennent à de plus fortes densités à l'extérieur du Parc National de Hwange parce que les éléphants y sont en densités moins élevées à cause du dérangement anthropique. Nous suspectons que les hautes densités d'éléphants dans le parc national ont causé la dégradation des savanes arborées ouvertes, habitat de l'hippotrague noir. Il n'y a cependant pas d'évidence d'un tel processus à l'échelle des paysages dans le Parc National de Hwange (Valeix et al., 2007b). C'est peut-être que l'effet des hautes densités d'éléphant sur l'habitat de l'hippotrague noir s'est exprimé à une autre échelle, e.g. disparition de la savane arborée dans les environs des points d'eau (de Beer et al., 2006; mais voir Chamaillé-Jammes et al., 2009), ou altération de l'organisation et du fonctionnement de la strate herbacée (Parker et al., 2009). Les éléphants sont de surcroit des compétiteurs alimentaires potentiels pour les hippotragues noirs. En effet, lorsque les éléphants s'alimentent sur la strate herbacée, ils prélèvent les hautes herbes, nourriture des hippotragues noirs (Bothma et al., 2002). Le mécanisme par lequel l'éléphant a peut-être influencé les patrons spatiaux et temporels des densités de grands herbivores dans notre aire d'étude mérite donc davantage de recherche.

A la question « est-ce que les zones de chasse en Afrique peuvent jouer un rôle de conservation des populations de grands herbivores ? », l'exemple du complexe de chasse de Matetsi nous incite à répondre oui. Il serait cependant imprudent de généraliser à l'ensemble des zones de chasse d'Afrique. Le complexe de chasse de Matetsi, sous l'autorité de l'état zimbabwéen, en collaboration avec des compagnies de chasse, a historiquement fait l'objet de suivis populationnels réguliers (i.e. comptages annuels aériens, et routiers), de taux de prélèvements généralement bas (i.e. ca. 2% de l'ensemble de la population par année, et ca. 10% du segment mâle de la population par année), et d'une gestion soutenue (e.g. contrôle de la longueur des cornes et ajustement des quotas de chasse, approvisionnement en eau, patrouilles anti-braconnage). C'est là un investissement en temps et en argent conséquent, réalisé notamment grâce aux retombées économiques engendrées par la chasse aux trophées. De plus, les zones de chasse de l'étude ont peut-être joué le rôle inattendu de refuge pour les grands herbivores contre les prédateurs et les hautes densités d'éléphants. Ceci pourrait en partie expliquer pourquoi les densités de grands herbivores y sont aujourd'hui autant, voire plus élevées que dans le Parc National de Hwange.

PORTÉE DES RÉSULTATS

Pour les études comportementales dans les populations exploitées ou perturbées par les activités anthropiques

L'un des principaux résultats de ma thèse est la mise en évidence d'ajustements comportementaux en réponse au risque de chasse, ajustements qui contrarient l'acquisition des ressources. Au delà de ce constat, cette thèse montre que l'amplitude de ces ajustements est limitée par la nécessité de maintenir l'acquisition des ressources clefs, et par la contrainte de ne pas s’exposer davantage aux prédateurs naturels en essayant d’éviter les chasseurs. C’est l’approche multi spécifique qui a permis de révéler pourquoi et comment il n’y a pas systématiquement ajustement comportemental en réponse au risque de chasse. En effet, lorsque les contraintes environnementales changent selon les espèces étudiées, l’amplitude des ajustements comportementaux en réponse à la perturbation humaine change aussi. Comme cette thèse le montre, certaines espèces peuvent ajuster leurs comportements, d’autres moins, voire pas.

La possibilité d’ajuster les comportements devrait de plus varier dans le temps avec l’intensité des contraintes environnementales, qui peuvent changer selon le moment de la journée et selon la saison. De même, à l’échelle individuelle, l’ajustement à la perturbation devrait varier selon le sexe, l’âge, le statut reproducteur, ou encore la condition corporelle des individus (revue dans Stankowich, 2008). L’absence d’ajustement comportemental ne signifie donc pas nécessairement absence de perturbation. Pour renseigner justement sur le degré de perturbation humaine subie par les animaux, l’approche comportementale doit être multi spécifique lorsque possible, utiliser des indices comportementaux relevés à diverses échelles de temps, et sur des individus différents. De plus, les données physiologiques (e.g. concentration en hormones de stress, taux métabolique, température corporelle) devrait être utilisées en complément à l’approche comportementale, et s’avérées être particulièrement pertinentes lorsqu’aucun ajustement comportemental n’est détecté. Ces recommandations dépassent le cadre des populations d’ongulés africains chassées pour les trophées, et sont valables pour les populations animales susceptibles d’être dérangées par les activités humaines en général.

Pour la gestion de la taille des cornes et autres traits phénotypiques sélectionnés par les chasseurs de trophées

Cette thèse est l’un des rares exemples d’étude des tendances à long terme de la taille des cornes dans les populations d’ongulés chassées pour les trophées, particulièrement en Afrique. Elle montre qu’à des taux de prélèvement de mâles adultes relativement bas (i.e. de l’ordre de 10% par année dans cette étude), le déclin des cornes n’est pas systématique, et que si déclin il y a, il est d’amplitude bien moindre (i.e. moins de 10%) que celui précédemment observé chez les mouflons américains et européens. Les exemples de l’impala et du grand koudou suggèrent même que le déclin peut être réversible à condition de diminuer le taux de prélèvement de mâles dans les populations chassées. Là encore, l’approche multi spécifique est prometteuse. Cette thèse montre comment la valeur commerciale de l’espèce chassée, en dictant le taux de prélèvement de mâles adultes, peut déterminer la tendance de la taille des cornes observées, i.e. les espèces les plus prisées sont celles qui subissent les taux de prélèvements susceptibles d’occasionner une diminution de la taille des cornes. En témoigne la situation de l’hippotrague noir, antilope emblématique d’Afrique australe, très prisée des chasseurs aux trophées. Les résultats semblent indiquer que le déclin de la taille des cornes chez cette espèce a une base génétique. Le principe de précaution recommanderait donc une diminution des taux de prélèvement sur cette espèce, voire un changement de mode de chasse en faveur de prélèvements de mâles aux petites cornes. La situation est d’autant plus préoccupante que l’espèce se raréfie dans la région, notamment dans le Parc National de Hwange. Le risque pour cette espèce, est que l’enjeu de sa conservation s’oppose aux intérêt économiques immédiats, parce que la valeur commerciale d’une espèce, et donc la pression de chasse exercée sur cette dernière, augmentent à mesure que l’espèce se raréfie (Palazy et al., 2011).

Pour schématiser, deux stratégies économiques s’opposent dans la gestion d’une zone de chasse, i.e. la recherche de bénéfices à court terme *vs* à long terme. Si l’objectif est d’engendrer un maximum de bénéfices à court terme, il est probable que le déclin de la taille des cornes et la raréfaction d’une espèce ne soient pas des arguments suffisants pour inciter les gestionnaires à baisser les quotas de chasse. En revanche, si l’exploitation de la zone se fait à moyen et long terme, les gestionnaires devraient être davantage préoccupées par un déclin de la taille des cornes et une raréfaction des espèces chassées. Sur le long terme en effet, il devrait être rentable de diminuer parfois les taux de prélèvement, afin de laisser le temps aux populations de se reconstituer et de générer des mâles aux grandes cornes. A cet égard, la durée d’exploitation accordée aux concessionnaires de zones de chasse par l’état dicte certainement le type de gestion adopté. Ainsi, les concessions qui n’ont l’exploitation de leur zone de chasse que pour quelques années devraient être moins enclines à sacrifier des quotas de chasse pour des retombées économiques futures dont elles ne bénéficieront pas. La composante économique doit donc être intégrée à l’étude des tendances temporelles de la taille des cornes dans les populations de grands herbivores chassées pour les trophées. Une meilleure gestion des populations animales exploitées passe en effet par l'évaluation des conséquences économiques d'un déclin du trait physique recherché (e.g. baisse de la biomasse des stocks de poissons pêchés; revue dans Jørgensen et al., 2007).

Avis aux gestionnaires : données pour suivre au mieux les populations chassées

Les suivis à long terme sont essentiels à la gestion des populations animales. Le complexe de chasse de Matetsi a fait l'objet de comptages réguliers par transects routiers depuis les années 1970. Ceux-ci ont permis de suivre les tendances de densité, démographie, pression de chasse des différentes espèces exploitées, et d'ajuster les quotas en conséquence. Ce type de données manque néanmoins pour les autres zones de chasse autour du Parc National de Hwange, i.e. les zones privées de *Gwaii Intensive Conservation Area,* et les zones communales de Tsholotsho où le programme CAMPFIRE est en place depuis les années 1990. De même, nous n'avons pas eu accès aux données de taille des cornes des animaux prélevés dans ces zones, soit parce qu'elles n'existaient pas, soit parce qu'elles n'avaient pas encore été numérisées. Nous encourageons donc la mise en place de comptages routiers dans ces zones, ainsi que la mesure systématique des cornes des mâles abattus. Ces données permettront d'évaluer les effets des différents régimes fonciers sur les densités, la démographie des populations exploitées, et la taille des cornes des mâles prélevés.

De même, sur les cornes des mâles récoltés, en plus de la longueur de la base à la pointe, nous insistons sur la nécessité de prendre systématiquement la circonférence de la corne à la base, la longueur entre les deux pointes, et d'autres mesures répertoriées dans les livrets d'enregistrement des trophées du *Safari Club International*[17] et du *Rowland Ward*[18]. En effet, la longueur des cornes n'est pas le seul trait susceptible de changer avec les années dans les populations d'ongulés chassées pour les trophées (Garel et al., 2007).

Si le coût des comptages routiers est jugé prohibitif (bien que moindre que les comptages aériens) par les autorités et gestionnaires locaux, des alternatives et méthodes

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[17] http://member.scifirstforhunters.org/static/RB/Methods/.

[18] http://www.rowlandward.com/content/default.aspx?pid=24&MainPage=2&SubPage=4.

complémentaires sont envisageables. Tout d'abord, la fréquence de ces comptages peut être réduite, à un comptage tous les deux ou trois années par exemple. Notons néanmoins que pour des espèces comme beaucoup d'ongulés, dont le cycle de vie est fondé sur un pas de temps annuel, il reste préférable d'effectuer des compatges chaque année. Ensuite, des comptages annuels aux points d'eau pourraient être mis en place dans les zones de chasse, à l'instar de ceux menés par la *Wildlife Environment Zimbabwe* depuis 1967 dans le Parc National de Hwange. Il s'agit d'un suivi de 24H00 aux points d'eau, répété chaque année lors de la pleine lune coïncidant avec le pic de la saison sèche (fin septembre - début octobre). Les données de suivis aux points d'eau fournissent des indices d'abondance de populations utiles pour suivre les tendances sur de longues séries temporelles. D'autre part, lors des observations aux points d'eau, il est plus aisé de déterminer la taille et la structure des groupes que lors des comptages routiers. C'est donc un bon moyen de récupérer des données fines sur la structure des populations, i.e. classes d'âge, rapport des sexes, proportion de juvéniles, etc.

L'accès aux carcasses d'animaux prélevés en zones de chasse donne l'opportunité de récupérer des données difficilement mesurables sur les animaux vivants. A *Matetsi Safari Area*, la masse éviscérée des animaux prélevés n'a plus été pesée depuis 1984. C'est pourtant une donnée essentielle, non seulement pour suivre la qualité des trophées dans le temps, mais aussi la condition corporelle des individus. De même, d'autres indices de condition corporelle facilement mesurables pourraient être utilisés, comme l'épaisseur du gras de la fesse par exemple. Ces indices sont un bon moyen de suivre la santé d'une population, parce qu'ils intègrent l'effet du climat, de l'habitat et des densités de compétiteurs intra et inter spécifiques.

Chasse aux trophées et conservation en Afrique

Cette thèse est l'une des rares études illustrant les effets à long terme de la chasse aux trophées sur les ongulés africains. Les tendances temporelles de taille de cornes et des densités de populations n'indiquent pas un effet marqué de la chasse aux trophées sur les populations chassées dans le complexe de chasse de la *Matetsi Safari Area*. Dans un contexte où les populations de grands ongulés déclinent dans la plupart des aires protégées d’Afrique (revue dans in Caro et Scholte, 2007; Western et al., 2009; Craigie et al., 2010), ces résultats illustrent le rôle de conservation que peuvent jouer les zones de chasse.

Il ne s’agit pas néanmoins de généraliser l’exemple de la *Matetsi Safari Area* à toutes les zones de chasse du Zimbabwe, et de l’Afrique. Signalons en effet que cette zone a fait l’objet d’une gestion raisonnée et soutenue par les autorités locales et les partenaires cynégétiques, i.e. suivis annuels de populations, ajustements des quotas de chasse, lutte anti braconnage, approvisionnement en eau, etc. La trajectoire des populations chassées dans les autres zones de chasse du pays, i.e. non administrées par les autorités locales mais par des propriétaires privés et par les communautés locales, pourrait être tout autre. A ce titre, les derniers inventaires aériens montrent que les densités des grands ongulés ont largement décliné dans ces zones aux cours des dernières années. Les autorités de la *Zimbabwe Wildlife Management Authority* ont repris les mesures systématiques de la taille des trophées (abandonnées depuis plusieurs années) dans ces zones de chasse. On pourra donc sous peu analyser les tendances temporelles de taille des cornes dans ces zones.

SYNTHÈSE GÉNÉRALE

La chasse aux trophées altère les comportements des individus et leur approvisionnement, peut réduire la proportion de mâles adultes, et diminuer la taille des cornes des mâles dans les populations chassées. Toutefois, l’amplitude de ces effets paraît être limitée lorsque les taux de prélèvements pratiqués sont relativement bas (i.e. de l’ordre de 2% de l’ensemble de la population par année, et 10% du segment mâle de la population par année dans notre étude). Cette thèse illustre comment plusieurs décennies de chasse aux trophées ne résultent pas forcément en une diminution de la taille des cornes des mâles, et un déclin des populations. Ceci a des implications sur le plan de la conservation des grands herbivores chassés pour leurs cornes, en Afrique et dans le reste du monde.

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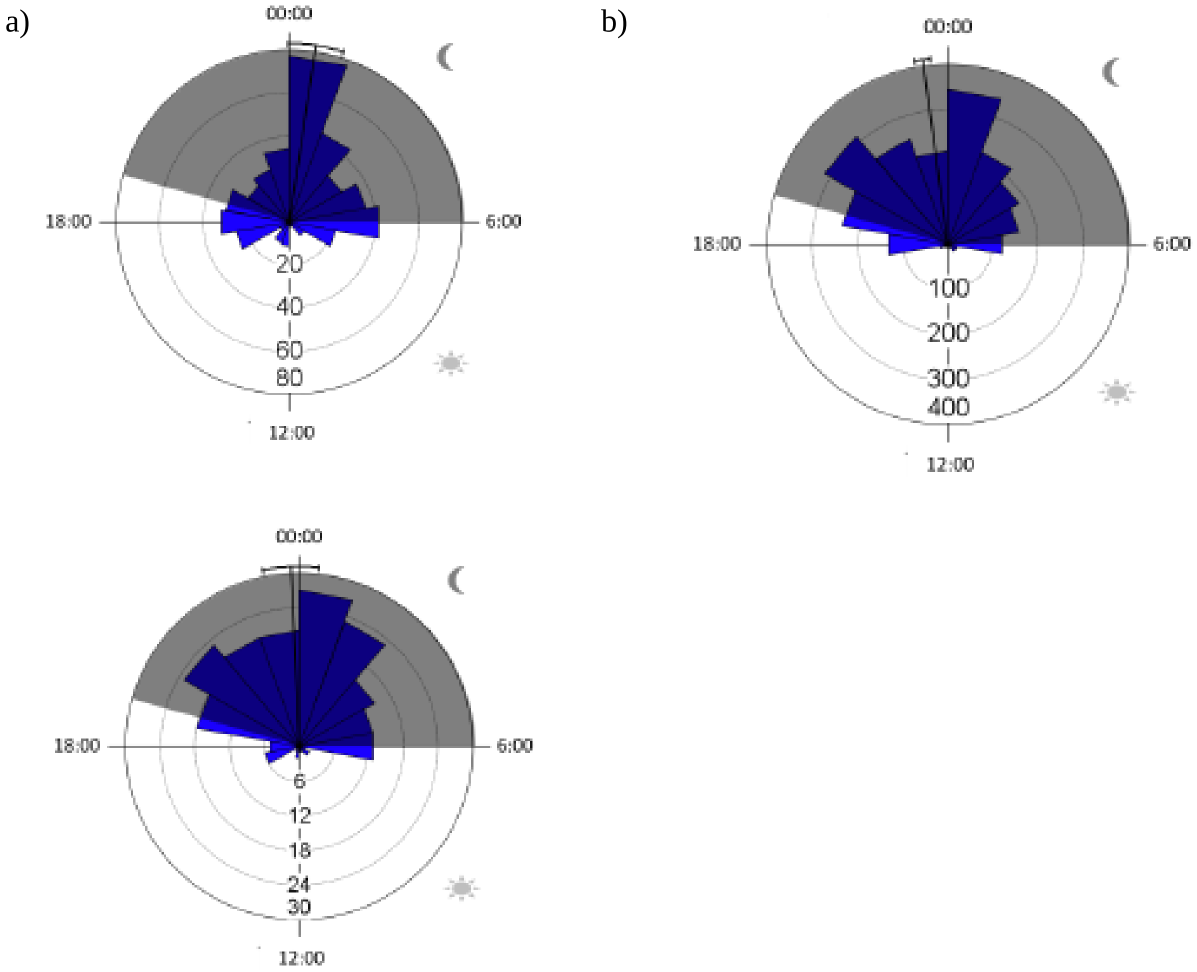
ANNEXES

Appendix 2.1



Temporal visits at the waterholes of Hwange National Park, Zimbabwe, by a) lions, b) spotted hyaenas, and b) leopards between 1994 and 2010 during daytime (6am to 7pm) and night time (7pm to 6am). Each bar length represents the number of observations at waterholes during each hour and the area of each bar is thus proportional to the frequency of observations. The black line underneath each graph indicates mean arrival time, with 95% confidence interval. Data were provided by the Wildlife Environment Zimbabwe (WEZ).

Appendix 3.1

Correlations between time spent walking, time spent in vigilance and time spent drinking relative to each phase of the use of waterholes (i.e. approach, drinking, and departure) by individual impala, greater kudu, and sable antelopes in Hwange National Park and the peripheral hunting areas, Zimbabwe.

Species			
	Impala	Greater kudu	Sable antelope
Approach phase	r = -0.96, *t* = -18.8	r = -0.95, *t* = -19.0	r = -0.99, *t* = -45.3
(walking vs vigilance)	df = 33, *P* < 0.0001	df = 35, *P* < 0.0001	df = 24, *P*<0.0001
Drinking phase	r = -0.81, *t* = -10.1	r = -0.84, *t* = -11.6	r = -0.84, *t* = -6.9
(drinking vs vigilance)	df = 51, P < 0.0001	df = 55, *P* < 0.0001	df = 20, *P* < 0.0001
Departure phase	r = -0.88, *t* = -10.5	r = -0.94, *t* = -14.1	r = -0.98, *t* = -25.7
(walking vs vigilance)	df = 31, *P* < 0.0001	df = 26, *P* < 0.0001	df = 32, *P* < 0.0001

Time spent by individuals in each behaviour was monitored throughout 2-min focal observations. We used Pearson correlation statistics to perform comparisons. The proportions of time spent in each behaviour have been square-root and arcsine transformed to meet assumptions of normality and homogeneity of variance (Sokal and Rohlf, 1995).

Appendix 3.2

Model selection procedure to estimate the drinking probability of groups, the proportion of time individuals spent in vigilance, and the time groups spent during the three phases at waterholes (i.e. approach, drinking, and departure) in Hwange National Park (HNP, hunting-free area), Zimbabwe, and in some peripheral hunting areas (HA), during the dry season 2008, for impala, greater kudu and sable antelope. The dependant variables are land use (HNP *vs* HA), group size, status (presence of juveniles *vs* no juveniles), and distance to cover (minimal distance to vegetation cover).

	Impala			Greater kudu			Sable antelope		
Dependant variables and models	k^a	AICc	ΔAICc	*k*	AICc	ΔAICc	*k*	AICc	ΔAICc
Group drinking probability									
land use + group size + status + distance to cover	19	194	5,6	18	175,9	1,6	15	14,8	6
land use X group size	18	190	1,6	17	176,1	1,8	14	17	8,2
land use X status	18	196,5	8,1	17	176,9	2,6	14	17,3	8,5
land use X distance to cover	***18***	***188,4***	***0***	17	178,5	4,2	14	12,8	4
land use + group size	17	193,9	5,5	16	175	0,7	13	15	6,2
land use + status	17	194,7	6,3	16	179,5	5,2	13	15,3	6,5
land use + distance to cover	17	191	2,6	16	179,1	4,8	13	10,8	2
land use	16	192,8	4,4	15	178,9	4,6	12	13,7	4,9
group size	16	192	3,6	***15***	***174,3***	***0***	12	13,6	4,8
status	16	192,9	4,5	15	179,2	4,9	12	13,6	4,8
distance to cover	16	192,6	4,2	15	178,8	4,5	12	8,8	0
null	15	191,1	2,7	14	178,7	4,4	***11***	***10,6***	***1,8***
Individual vigilance in approach									
land use + group size + status + sex + distance to cover	13	67,2	37,2	13	39,6	28,8	13	37,8	35,4
land use X group size	11	52,1	22,1	11	26,6	15,8	11	22,2	19,8
land use X status	11	30	0	11	16,9	6,1	11	8,4	6
land use X sex	11	38,8	8,8	11	20,5	9,7	11	10,9	8,5
land use X distance to cover	11	51	21	11	35,2	24,4	11	23,9	21,5

land use + group size	10	43,3	13,3	10	20	9,2	10	13,1	10,7
land use + status	10	34,7	4,7	10	13,2	2,4	10	7,3	4,9
land use + sex	10	35,7	5,7	10	16,5	5,7	10	4,1	1,7
land use + distance to cover	10	43,7	13,7	10	23,6	12,8	10	13,4	11
land use	***9***	***30,8***	***0,8***	***9***	***10,8***	***0***	***9***	***2,4***	***0***
group size	9	45,3	15,3	9	22,6	11,8	9	12,4	10
status	9	36,2	6,2	9	16,6	5,8	9	7	4,6
sex	9	37,4	7,4	9	18,7	7,9	9	6,7	4,3
distance to cover	9	44,3	14,3	9	24,9	14,1	9	13,4	11
null	8	33	3	8	13,3	2,5	8	4,9	2,5
Individual vigilance in drinking									
land use + group size + status + sex + distance to cover	13	23,9	35	14	26,8	39,2	14	44,2	42,8
land use X group size	11	10,7	21,8	12	11,4	23,8	12	28,5	27,1
land use X status	11	0,2	11,3	12	1,4	13,7	12	17,1	15,7
land use X sex	11	–0,1	11	12	1,6	13,9	12	18,3	16,9
land use X distance to cover	11	10,1	21,2	12	17,6	29,9	12	32,4	31
land use + group size	10	1,5	12,6	11	3,7	16,1	11	19,1	17,7
land use + status	10	–5	6,1	11	–0,5	11,8	11	12,9	11,5
land use + sex	10	–4,7	6,4	11	–3,3	9	11	12,8	11,4
land use + distance to cover	10	–1	10,1	11	7,6	19,9	11	19,7	18,3
land use	***9***	***–11,1***	***0***	10	–6,5	5,8	10	7,2	5,8
group size	9	3,7	14,8	10	–2,1	10,2	10	13,5	12,1
status	9	–3,1	8	10	–6,4	5,9	10	6,9	5,5
sex	9	–3	8,1	10	–9,3	3	10	6,6	5,2
distance to cover	9	–0,6	10,5	10	2	14,4	10	14,3	12,9
null	8	–8,6	2,5	***9***	***–12,3***	***0***	***9***	***1,4***	***0***
Individual vigilance in departure									
land use + group size + status + sex + distance to cover	13	48,9	32,2	16	54,9	37,6	15	19,5	27,5
land use X group size	11	34,6	17,9	14	35,4	18	13	9,9	17,9
land use X status	11	24,2	7,5	14	29,3	12	13	–1,4	6,6

land use X sex	11	25,9	9,2	14	29,7	12,4	13	1,1	9,1
land use X distance to cover	11	40,4	23,7	14	47,4	30	13	11	19
land use + group size	10	26	9,3	13	30,1	12,8	12	4	12
land use + status	10	21,3	4,6	13	26,2	8,8	12	–3,7	4,3
land use + sex	10	21,9	5,2	13	27	9,7	12	–1,7	6,3
land use + distance to cover	10	29,6	12,9	13	35,8	18,4	12	–1,5	6,5
land use	***9***	***16,7***	***0***	12	21,9	4,5	***11***	***–8***	***0***
group size	9	25,7	9	12	25,4	8,1	11	4,7	12,7
status	9	22,9	6,2	12	21,3	3,9	11	–3	5
sex	9	24,5	7,8	12	22,2	4,9	11	–1,7	6,3
distance to cover	9	31,3	14,6	12	31,1	13,8	11	1,2	9,2
null	8	19,4	2,7	***11***	***17,3***	***0***	10	–5,4	2,6
Group approach time									
land use + group size + status + distance to cover	28	441,7	18,8	35	325,7	19,9	20	136,8	18,2
land use X group size	27	442,9	20	34	320,6	14,8	19	137,1	18,5
land use X status	27	431,7	8,8	34	311,3	5,5	19	123,5	4,9
land use X distance to cover	27	438,3	15,4	34	322	16,2	19	137	18,4
land use + group size	26	434,4	11,5	33	315,7	9,9	18	130,7	12,1
land use + status	26	428,7	5,8	33	310,7	4,9	18	121,9	3,3
land use + distance to cover	26	428,5	5,6	33	314,5	8,7	18	128,7	10,1
land use	25	424,5	1,6	32	307,5	1,7	17	120,7	2,1
group size	25	432,8	9,9	32	314	8,2	17	128,5	9,9
status	25	427	4,1	32	308,9	3,1	17	119,7	1,1
distance to cover	25	427	4,1	32	312,6	6,8	17	126,4	7,8
null	***24***	***422,9***	***0***	***31***	***305,8***	***0***	***16***	***118,6***	***0***
Group drinking time									
land use + group size + status + distance to cover	17	355,1	14,7	20	243,2	22,2	14	138,7	13,6
land use X group size	16	342,4	2	19	236,2	15,2	13	134,8	9,7
land use X status	16	380	39,6	19	227,4	6,4	13	130,5	5,4
land use X distance to cover	16	394,3	54	19	247,5	26,5	13	144,9	19,8

land use + group size	***15***	***340,4***	***0***	18	231,4	10,4	12	129,2	4,1
land use + status	15	376,3	36	18	224,4	3,4	12	130	4,9
land use + distance to cover	15	384,5	44,1	18	238,1	17,1	12	136,4	11,3
land use	14	376	35,6	17	228,1	7,1	11	127,9	2,8
group size	14	342,1	1,7	17	227,5	6,5	11	126,4	1,3
status	14	380,4	40	***17***	***221***	***0***	11	126,9	1,8
distance to cover	14	390,7	50,3	17	234,2	13,2	11	134,7	9,6
null	13	380,2	39,9	16	224,3	3,3	***10***	***125,1***	***0***
Group departure time									
land use + group size + status + distance to cover	31	440,2	23,9	22	321	15,7	20	147,5	19,6
land use X group size	30	433,8	17,5	21	313,1	7,8	19	145,7	17,8
land use X status	30	422,9	6,6	21	307,9	2,6	19	131	3,1
land use X distance to cover	30	434,8	18,5	21	328,8	23,5	19	144,6	16,7
land use + group size	29	425,6	9,3	20	308,2	2,9	18	139,4	11,5
land use + status	29	420,6	4,3	20	306,2	0,9	18	131,1	3,2
land use + distance to cover	29	427,1	10,8	20	320,5	15,2	18	137,2	9,3
land use	28	416,3	0	19	310,1	4,8	17	131,9	4
group size	28	426,2	9,9	19	307,6	2,3	17	136,5	8,6
status	28	421,4	5,1	***19***	***305,3***	***0***	17	127,9	0
distance to cover	28	427,4	11,1	19	318,9	13,6	17	135,7	7,8
null	***27***	***417***	***0,7***	18	308,7	3,4	***16***	***129***	***1,1***

The selected models (lowest AICc) are shown in bold font.

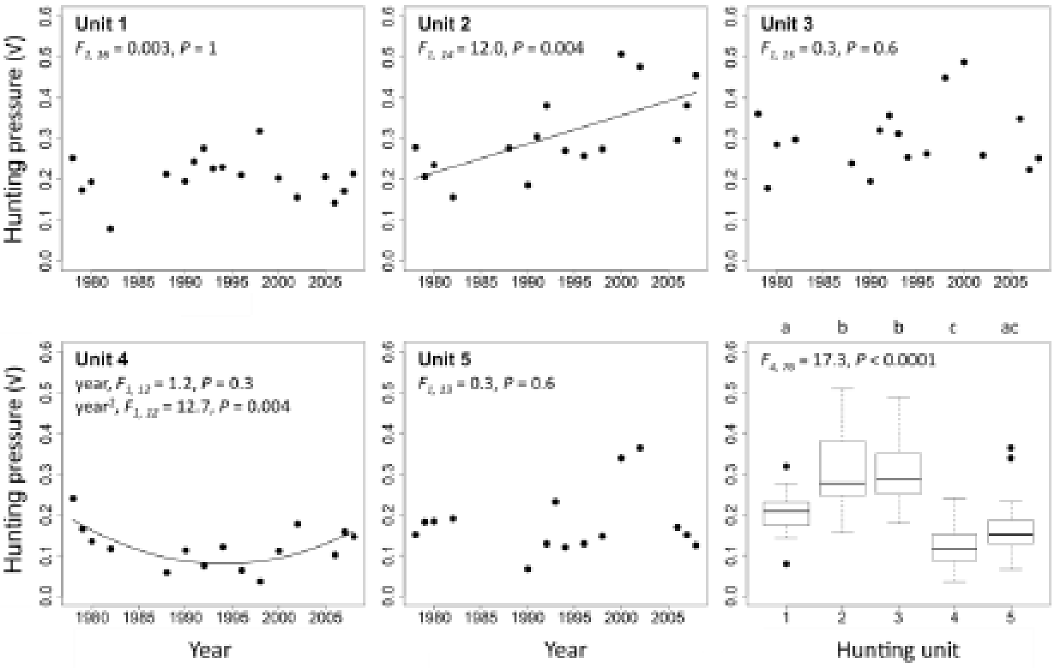
[a] Number of parameters. It includes the random factor “waterholes”, and the random factor “approach or departure distances” for the group approach and departure times.

Appendix 4.1

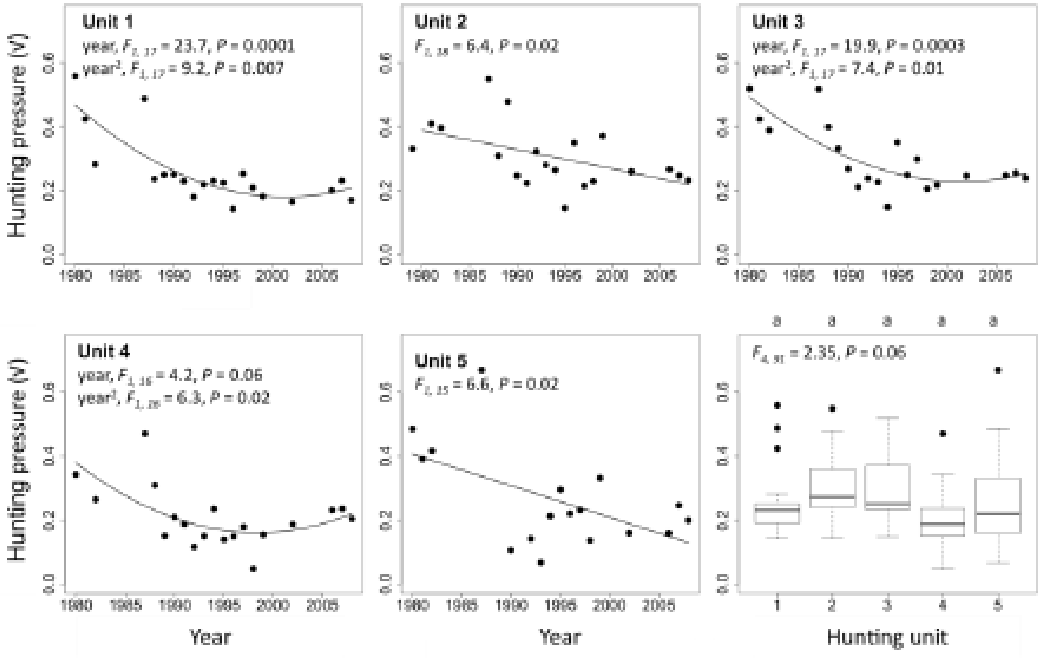
Because hunting quotas are determined annually and allocated per hunting unit, we calculated yearly estimates of trophy hunting pressure (i.e. number of adult males harvested / estimated number of adult males in the population) within each hunting unit. We used simple linear models to investigate temporal trends of 1) trophy hunting pressure (Appendix 4.1a), and 2) population densities (log-transformed) (Appendix 4.1b), for each species in each unit. We then compared hunting pressure and densities among hunting units for each species (Appendixes 4.1a and 4.1b), and trophy hunting pressure among species, using ANOVAs with hunting unit, and species as single factors. We used Tukey Honest Significant Differences statistics for multi-comparisons.

a)

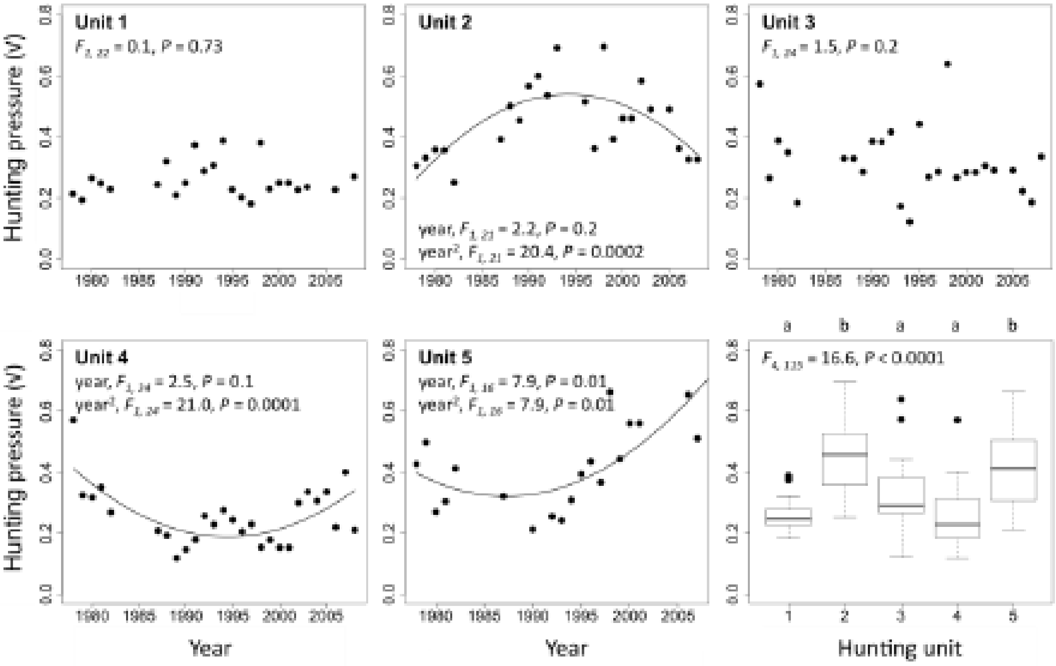
i)


Unit 1
$F_{1,18}$ = 0.003, P = 1
Unit 2
$F_{1,14}$ = 12.0, P = 0.004
Unit 3
$F_{1,15}$ = 0.3, P = 0.6
Unit 4
year, $F_{1,12}$ = 1.2, P = 0.3
year^2, $F_{1,12}$ = 12.7, P = 0.004
Unit 5
$F_{1,13}$ = 0.3, P = 0.6
$F_{4,70}$ = 17.3, P < 0.0001
a
b
b
c
ac
Hunting pressure (V)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
1980
1985
1990
1995
2000
2005
Year
1
2
3
4
5
Hunting unit

ii)

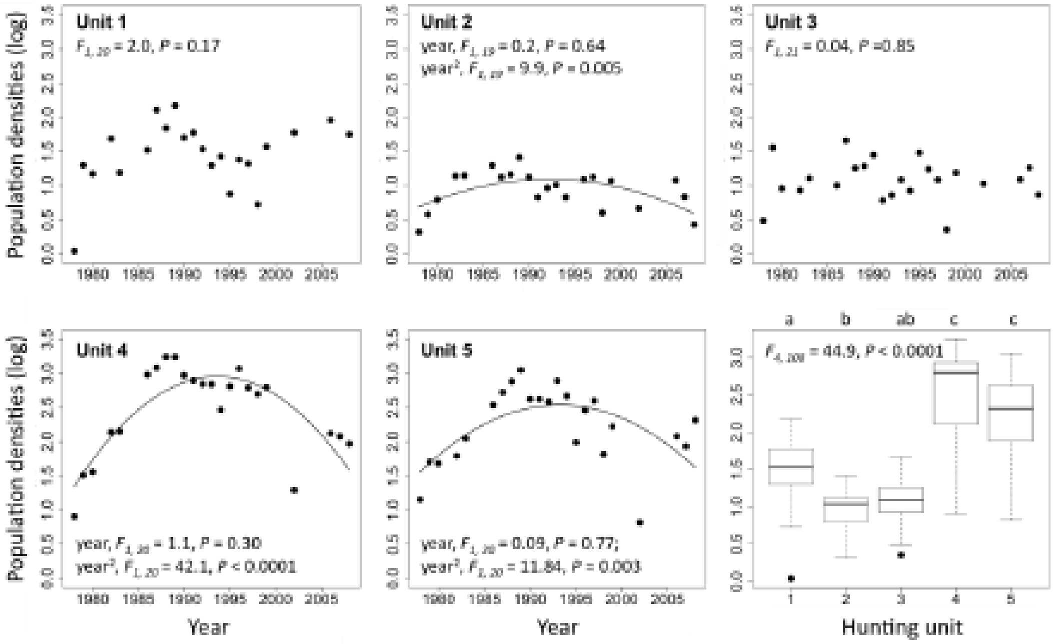

Unit 1
year, $F_{1,17}$ = 23.7, P = 0.0001
year^2, $F_{1,17}$ = 9.2, P = 0.007
Unit 2
$F_{1,18}$ = 6.4, P = 0.02
Unit 3
year, $F_{1,17}$ = 19.9, P = 0.0003
year^2, $F_{1,17}$ = 7.4, P = 0.01
Unit 4
year, $F_{1,16}$ = 4.2, P = 0.06
year^2, $F_{1,16}$ = 6.3, P = 0.02
Unit 5
$F_{1,15}$ = 6.6, P = 0.02
$F_{4,91}$ = 2.35, P = 0.06
a
a
a
a
a
Hunting pressure (V)
0.0
0.2
0.4
0.6
1980
1985
1990
1995
2000
2005
Year
1
2
3
4
5
Hunting unit

iii)

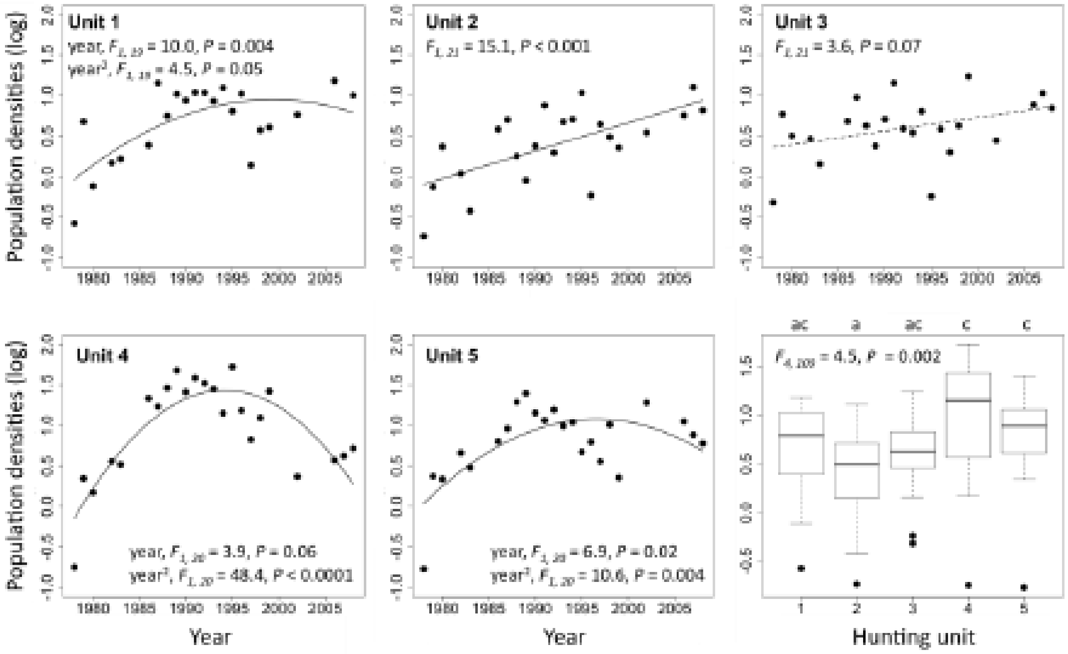

Unit 1
$F_{1,22}$ = 0.1, P = 0.73
Unit 2
year, $F_{1,21}$ = 2.2, P = 0.2
year^2, $F_{1,21}$ = 20.4, P = 0.0002
Unit 3
$F_{1,24}$ = 1.5, P = 0.2
Unit 4
year, $F_{1,24}$ = 2.5, P = 0.1
year^2, $F_{1,24}$ = 21.0, P = 0.0001
Unit 5
year, $F_{1,16}$ = 7.9, P = 0.01
year^2, $F_{1,16}$ = 7.9, P = 0.01
$F_{4,115}$ = 16.6, P < 0.0001
a
b
a
a
b
Hunting pressure (V)
0.0
0.2
0.4
0.6
0.8
1980
1985
1990
1995
2000
2005
Year
1
2
3
4
5
Hunting unit

b)

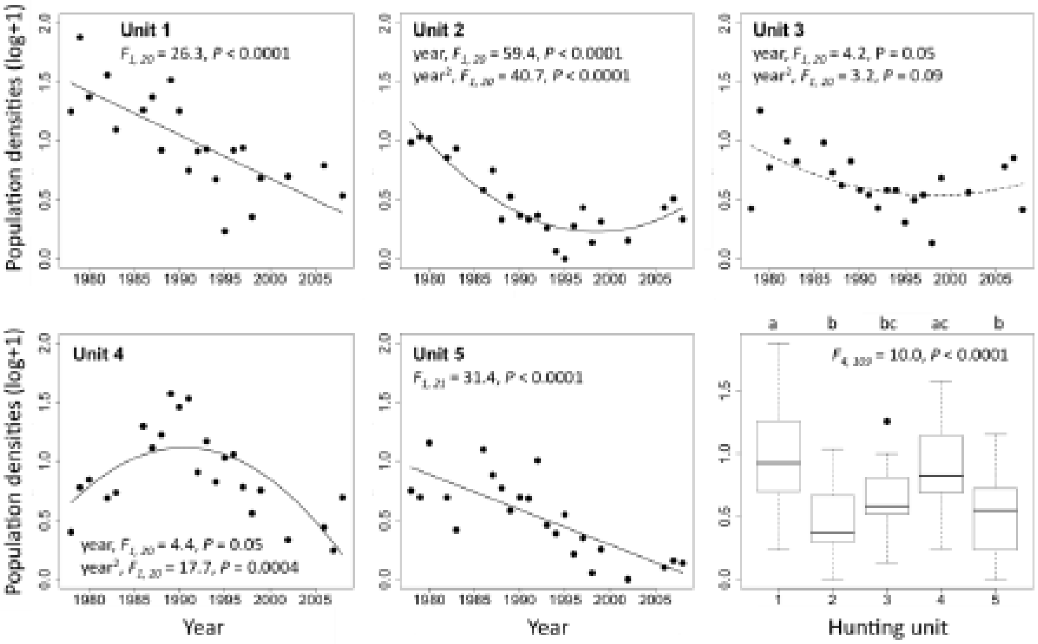
i)


Unit 1
F1, 20 = 2.0, P = 0.17
Unit 2
year, F1, 19 = 0.2, P = 0.64
year², F1, 19 = 9.9, P = 0.005
Unit 3
F1, 21 = 0.04, P =0.85
Unit 4
year, F1, 20 = 1.1, P = 0.30
year², F1, 20 = 42.1, P < 0.0001
Unit 5
year, F1, 20 = 0.09, P = 0.77;
year², F1, 20 = 11.84, P = 0.003
a
b
ab
c
c
F4, 108 = 44.9, P < 0.0001
Population densities (log)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
1980
1985
1990
1995
2000
2005
Year
1
2
3
4
5
Hunting unit

ii)


Unit 1
year, F1, 19 = 10.0, P = 0.004
year², F1, 19 = 4.5, P = 0.05
Unit 2
F1, 21 = 15.1, P < 0.001
Unit 3
F1, 21 = 3.6, P = 0.07
Unit 4
year, F1, 20 = 3.9, P = 0.06
year², F1, 20 = 48.4, P < 0.0001
Unit 5
year, F1, 19 = 6.9, P = 0.02
year², F1, 20 = 10.6, P = 0.004
ac
a
ac
c
c
F4, 109 = 4.5, P = 0.002
Population densities (log)
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
1980
1985
1990
1995
2000
2005
Year
1
2
3
4
5
Hunting unit

iii)



Temporal trends of **a)** trophy hunting pressure (i.e. number of adult males harvested / estimated number of adult males in the population), and **b)** population densities (log-transformed), in hunting units one to five of Matetsi Safari Area, Zimbabwe, from 1978 to 2008, for i) impala, ii) greater kudu, and iii) sable antelope. Data points indicate annual values of densities. Continuous lines are used for significant trends ($P < 0.05$), dashed lines for almost-significant trends ($0.05 \leq P < 0.1$). No line indicates no trend ($P > 0.1$). The F statistics and P values are provided for each hunting unit. Box plots represent hunting pressure or population densities averaged over the study period for each species across the five hunting units. The horizontal line within the box represents the median, the box illustrates the range between the 25th and 75th percentiles, the two dotted segments outside the box represent the 10th and 90th percentiles, and the black dots are the observation <10th or >90th percentiles. Averaged hunting pressures and population densities are compared among hunting units for each species. Different letters indicate hunting pressures or population densities different at $P < 0.05$.

Appendix 6.1

Hwange National Park (HNP), ca. 15,000 km^2, is a state land administrated by Zimbabwe Parks and Wildlife Management Authority (ZPWMA) (Fig. 6.1). Permanent settlements are not allowed within the limits of the Park, aside from Park headquarters and some outlying ranger posts. ZPWMA also forbids natural resources extraction within the Park. National Park patrols are conducted regularly.

Matetsi Safari Area (MSA), ca. 7,500 km^2, stretches along the northwestern border of HNP up to the Zambian border (Fig. 6.1). MSA is also a state land administrated by ZPWMA, but leased to safari operators since 1973 for hunting tourism. No permanent human settlements are allowed in MSA, besides the few camps of safari operators that reside on their concessions all year long and limit illegal activities, as well as manage fire and surface water. Hunting quotas are set by ZPWMA. For large herbivores such as sable antelope, hunting quotas are set at approximately 2% of the population size, 0.5% for elephant (Cumming, 1989).

The Sikumi and Ngamo *Forest Areas* (FA), and the southern part of the *Gwaii Intensive Conservation Area* (Gwaii), constitute the buffer zone of HNP along its northeastern border, ca. 3,100 km^2 (Fig. 6.1). The FA are state lands administrated by the Forestry Commission, and allow timber and photographic as well as hunting tourism concessions. Permanent human settlements are not allowed, but villages and communal lands extend at their immediate periphery (Fig. 6.1). The proximity of these inhabited areas generates poaching, illegal livestock grazing, and illegal timber harvesting within the FA boundaries. Gwaii is a complex of private farms where hunting tourism is the main economic activity since the mid-1990s. Hunting quotas are set by ZPWMA. The control of illegal activities is at the discretion of the farm owners. As for the FA, villages and communal lands surround Gwaii, thus the area is strongly exposed to poaching and other illegal activities.

The *Tsholotsho communal lands* (Tsholotsho), ca. 8,000 km^2, extend at the southern boundary of HNP. This is the adjacent area to HNP where the impact of human development and use of resources is the highest (Peace Parks Foundation, 2009). Poverty levels are high, and rural communities strongly depend on natural resources to complete subsistence farming. Besides hunting, legalized under the CAMPFIRE program (Child, 1996), Tsholotsho maintains timber and related forestry products, commercial farms (i.e. crops, cattle, and wildlife), and pastoralism.

Appendix 6.2

Mean proportion (%±sd) of the main vegetation types, and of the availability of surface water, over the studied blocks of Hwange National Park (HNP) and of the immediate hunting areas (HA). The nonparametric Wilcoxon test was used to investigate whether there was any statistical difference between HNP and HA.

Vegetation types	HNP	HA	Wilcoxon test
Grassland	7.7±11.8	11.7±8.0	*W*=6, *P*=0.2
Open shrubland	19.0±14.6	33.5±17.6	*W*=6, *P*=0.2
Shrubland	16.6±15.3	5.0±6.4	*W*=19, *P*=0.2
Thicket	7.0±6.7	0.5±0.8	*W*=18, *P*=0.3
Water	26.7±11.1	33.2±16.8	*W*=10, *P*=0.7
Wooded habitats	48.4±18	48.4±12	*W*=14, *P*=0.8