

Poaching creates ecological traps within an iconic protected area

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Abstract

Ecological traps occur when areas preferentially selected by a species harbour an unknown increased mortality risk or reduced fitness for the individuals utilizing them. If animals continue to utilize these habitats, rapid declines may result that threaten the persistence of the population. Both black and white rhinoceroses are plagued by severe, targeted rhino poaching in South Africa that may have population and species-level consequences in the long term. Poaching can rapidly increase mortality and may create habitats that function as ecological traps for protected populations. We used spatially explicit data of live rhino and poached rhino carcasses in the Kruger National Park, South Africa, to define high- and low-risk states for both black and white rhino species. The proportion of area functioning as ecological trap was similar for both species (black: 37.73%, white: 35.51%), while the proportion of safe harbour was considerably lower for black rhino (black rhino: 32.01%, white rhino: 44.74%). Species-specific risk areas were condensed into management categories that reflect the actions most likely to be effective for overall rhino protection in those areas. 'Threat' area, representing ecological traps for both species, comprised 32.48% of southern Kruger; this represents the highest priority for anti-poaching interventions. A further 31.03% was identified as 'haven', representing safe harbours for both species, which may benefit most from continued rhino monitoring and surveillance. Using these categories, authorities can prioritize the distribution of limited resources and tailor anti-poaching and biological management actions according to the needs of each area for the concurrent protection of both rhino species. This work illustrates how the conservation of multiple species or taxa within a system can be simultaneously prioritized in vast areas where resources and/or capacity may be insufficient to undertake species-specific approaches.

Introduction

Understanding the drivers of species occurrence and habitat selection contributes to the conservation and management of wild populations (Johnson & Gillingham, 2005). This knowledge can provide insight into the complex nature of species-environment interactions, ecosystem function and population dynamics, and can often be used to explain or predict species performance (Morris, 2003). Habitat selection by wild herbivores reflects a combination of climatic, dietary and vegetation preferences, and is commonly influenced by factors such as surface water availability and vegetation quality (Fritz *et al.*, 1996; Muposhi *et al.*, 2016). Competition and predation risk may also impact herbivore distribution, particularly at a

local scale (Pulliam & Danielson, 1991; Valeix *et al.*, 2009). These factors create variability in habitat quality, with high-quality habitat conferring fitness advantages through increased reproductive potential and survival and low-quality habitat conferring fitness costs through reduced reproductive potential and survival (Delibes, Gaona, & Ferreras, 2001). In addition to ecological factors, modern anthropogenic disturbances such as fire, habitat degradation and infrastructure development can significantly affect habitat selection in particular areas (Abrams *et al.*, 2012; Robertson, Rehage, & Sih, 2013).

Within protected areas, the drivers of habitat selection should be dominated by ecological processes rather than modern anthropogenic disturbances, with high-quality habitat and the associated increased survival available for most

species. However, in recent years, the rapid growth of the illegal wildlife trade and corresponding increase in poaching within protected areas in many countries have placed enormous pressure on certain wildlife species. Poaching can rapidly increase mortality within a population and may be temporally or physically localized within a protected area (Woodroffe & Ginsberg, 2008). If poaching is persistently localized, and the increased mortality risk cannot be detected by animals, poaching may create habitats that function as ecological traps for protected populations (Abrams *et al.*, 2012). Ecological traps are areas or habitats that are equally or more attractive than others, but harbour an increased mortality risk or reduced fitness for the individuals utilizing them (Schlaepfer, Runge, & Sherman, 2002). Ecological traps may form when habitat quality cues remain unchanged but survival or fitness in an area is reduced, or habitat cues are distorted and no longer reflect the true habitat quality (Robertson & Hutto, 2006). If animals are unaware of the increased risk and continue to utilize these habitats, this can lead to rapid declines that threaten the persistence of the population, and ultimately, species (Abrams *et al.*, 2012; Fletcher, Orrock, & Robertson, 2012). Human-induced mortality such as poaching is an example of such a risk, and may act as a substantial population-level threat if it persists over long periods. From a conservation perspective, understanding the spatial patterns of habitat selection and human-induced mortality in protected populations of endangered species can enable the identification of high and low threat areas, the design of innovative management approaches and the optimal allocation of limited capacity and resources.

Recent work in this field has predominantly focused on large carnivores or omnivores with the identification of ecological traps for species such as brown bears *Ursus arctos* (Falcucci *et al.*, 2009; Northrup, Stenhouse, & Boyce, 2012; Lamb *et al.*, 2017; Penteriani *et al.*, 2018), Andean bears *Tremarctos ornatus* (Sánchez-Mercado *et al.*, 2014), jaguars *Panthera onca* (Romero-Muñoz *et al.*, 2018) and leopards *Panthera pardus* (Pitman *et al.*, 2015). These studies have focused on individual species where conservation strategies are needed to offset conflict-related deaths, primarily in human-modified landscapes. While methodologies and data types differ between studies, all make use of animal locations and mortality data to predict areas of high risk for the species in question. Poaching data, in conjunction with species occurrence data, have been used to identify ecological traps for Andean bears (Sánchez-Mercado *et al.*, 2014) and savanna elephants (Roever, van Aarde, & Chase, 2013) both inside and outside of the protected areas and rank areas for additional protection. It is not always possible, however, for management authorities to prioritize a single species within a protected area when others are also at risk, particularly when the threat is severe and/or requires significant resources to address.

Increasing demand for rhino horn to supply the illegal wildlife trade has resulted in relentless poaching of rhinoceroses in the last decade, particularly in South Africa (Emslie *et al.*, 2016). The Kruger National Park, South Africa, hosts the largest populations of two species: the

south-eastern black rhinoceros *Diceros bicornis minor*; hereafter black rhino and southern white rhinoceros *Ceratotherium simum simum*; hereafter white rhino, and is one of the few remaining free-ranging, 'natural' populations in the world. However, Kruger is plagued by severe, targeted rhino poaching which is likely to have population and species-level consequences in the long term (Ferreira, Greaver, & Knight, 2011; Ferreira *et al.*, 2018). The black rhinoceros is critically endangered, with less than 6000 animals remaining globally (Emslie *et al.*, 2016). Black rhino are elusive and difficult to monitor, and have been identified as a species of special concern within Kruger by South African National Parks (SANParks), due to their low numbers, declining growth and poaching losses experienced. The white rhino is currently listed as 'near threatened' on the IUCN Red List of Threatened Species (Emslie, 2012), with a global population of approximately 20 000 animals (Emslie *et al.*, 2016). Despite their large population size, white rhino have suffered the majority of the annual poaching fatalities over the last 5 years in South Africa (Emslie *et al.*, 2016), and the Kruger population shows a net annual decline (Ferreira *et al.*, 2018). Management within Kruger therefore need to utilize limited resources in a manner that protects both rhino species simultaneously. Identifying high and low threat areas common across both species may be the most practical way to ensure maximum impact in rhino protection and management.

Spatially explicit data of live rhino and poached rhino carcasses provide an opportunity to determine whether areas in the southern Kruger National Park function as ecological traps for rhinos. In this study, we identify areas with high and low probability of poaching (Nielsen *et al.*, 2006; Roever *et al.*, 2013; Sanchez-Mercado *et al.*, 2014) and relate these areas to rhino occurrence within the Kruger landscape. We expect that environmental variables will exert the primary influence on live rhino occurrence, and anthropogenic variables will be the key drivers of carcass occurrence. By overlaying these results, we classify high threat areas (ecological traps) and low threat areas (safe harbours) within southern Kruger according to the dual occurrence probability and mortality risk for each rhino species. Finally, we combine the species-specific risk areas into categories to inform innovative management interventions that would enable the optimal allocation of limited resources that maximizes the protection of both rhino species.

Materials and methods

Study area

The Kruger National Park (24°0'41" S, 31°29'7" E) is the largest protected area in South Africa and encompasses 19 485 km² of low-lying savanna. The landscape varies across the park, with landscape types classified according to vegetation type, soil and geological characteristics (Gertenbach, 1983). Black rhinos are predominantly found south of the Olifants river (Kruger, Reilly, & Whyte, 2008), most likely as a result of their reintroduction locations in southern Kruger. White rhino have a wider distribution across the

park, but occur at their highest densities in the southern region (Ferreira *et al.*, 2018).

Within the southern region, an Intensive Protection Zone (IPZ; Fig. 1) was established in 2014 to prioritize the security of rhino in high-density areas using advanced technology, equipment and infrastructure. The IPZ covers approximately 4000 km² and is comprised of nine landscape types, summarized as follows: Acacia thicket, Sabie/Crocodile thicket, Lowveld sour bushveld, mountain bushveld, mixed Combretum/Terminalia woodland, Combretum woodland, Acacia savanna, Lebombo south and thornveld (Gertenbach, 1983). Southern Kruger also suffers the greatest human incursion and poaching rates, likely as a result of high rhino densities, intensive human settlement along the boundary, international access and rudimentary fencing.

Rhino data

We used 5 years of rhino sightings data collected during annual aerial rhino surveys from 2013 to 2017 in the IPZ of the Kruger National Park. These surveys were conducted by Jet Bell Ranger helicopter in August and September each year, following a block-count approach; details can be seen in Ferreira *et al.* (2015). Approximately, 50% of the available 3 × 3 km blocks were surveyed each year and animal age, sex and GPS locations were recorded. Block selection was randomly distributed across each landscape type. By combining the annual data, we generated a spatially explicit dataset of 723 black rhino sightings and 12 921 white rhino sightings within the study area over a 5-year period. For poached rhino, we extracted carcass locations of animals killed between 2013 and 2017 from the large mammal carcass database maintained by the SANParks Environmental Crime Investigative (ECI) unit. Only rhino deaths recorded

as ‘shot’ were used in the analyses; unknown and natural deaths were removed. This resulted in poached carcass datasets of 81 black rhino and 1366 white rhino.

Live rhino and carcass occurrence

We used a resource selection function (RSF) approach and ran generalized linear models (GLMs) with a binomial error structure to investigate the environmental and anthropogenic variables influencing rhino occurrence and mortality in southern Kruger. In addition to our live rhino locations, we generated an equal number of random points within the census blocks to represent locations available to rhino. The binomial response variable was thus 0 (random point within the surveyed area) or 1 (rhino location). The predictor variables included in the models were: distance to main rivers, landscape type (Gertenbach, 1983); woody cover (for black rhino; Bucini, Saatchi, Hanan, Boone, & Smit, 2009) or herbaceous biomass (for white rhino; Smit, 2011); terrain ruggedness, distance to human activity (represented by ranger stations), distance to roads and distance to fence. Woody cover represents the percentage of tree and shrub cover (Bucini *et al.*, 2009), and herbaceous biomass is a co-kriged interpolated surface representing average forage quantity (Smit *et al.*, 2011). Terrain ruggedness is represented by the topographic position index (TPI) of each cell, calculated from a 90-m digital elevation model (DEM). Ranger stations house the rangers of each section and represent areas of permanent human activity. Distances were extracted from distance rasters produced using the ‘raster’ package (Hijmans, 2019) in R v3.5.1 (R Core Team, 2018). All variables were re-sampled to a 200 m × 200 m resolution. Prior to model selection, predictor variables were tested for collinearity using Pearson’s Correlation; no pairs of predictors showed

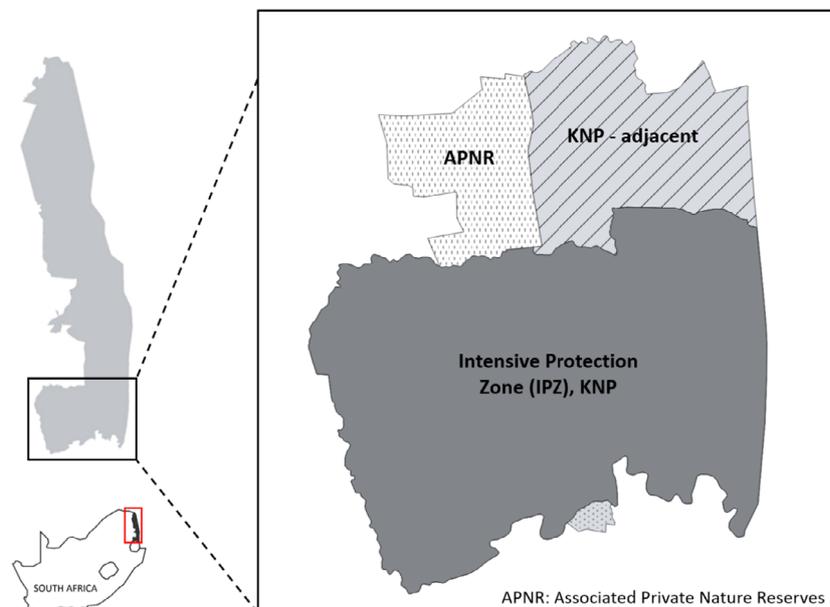


Figure 1 The Intensive Protection Zone (IPZ) within the southern Kruger National Park and surrounds. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

$r > 0.6$ and thus none were considered collinear. Models were run using the ‘glmulti’ package (Calcagno, 2019) in R v3.5.1 (R Core Team, 2018), and ranked by Akaike Information Criterion adjusted for sample size (AICc). Predictor variables remaining in the top models were tested for non-linear fit using quadratic terms or log transformation. Similarly, we used GLMs with a binomial error structure to test the influence of variables on poached rhino locations. Landscape type was, however, excluded from the mortality analyses as small clusters of carcasses greatly distorted landscape significance and collapsed the models. Detection probability of both live rhino and carcass occurrence was considered comparable as both are performed through extensive aerial surveillance in southern Kruger.

Landscape preference

We used Ivlev’s Selectivity Index (Krebs, 1999) to investigate the degree to which the landscape preferences of black and white rhino have been influenced by the removal of animals by poaching. Ivlev’s index represents a measure of the use of a landscape in relation to its availability. Values >0 indicate that the landscape is used proportionately more relative to the amount of that landscape available (preference), and values <0 indicate that a landscape is used proportionately less than it is available (avoidance). For each species, we compared the impacted population (consisting of live rhino sightings only) to a representation of the original population without the impact of poaching, that is, without animals removed (combined live rhino and carcass sightings). If poaching has removed a significant proportion of animals from a particular landscape and that landscape has not yet been recolonized to the same degree, the index of selectivity using only live sightings may not be a historic reflection of habitat preference. This may be particularly true for black rhino as they are typically slow to colonize new or empty habitat (Linklater & Hutcherson, 2010); the rapid removal of individuals from a localized area may leave that area devoid of animals for some time, thus appearing to be ‘avoided’. Conversely, white rhino move large distances and recolonize new habitats relatively easily (Norman Owen-Smith, 1983), thus the landscape preferences seen in the impacted population may be more similar to those of the original population. We used the comparisons between the original and impacted populations to further understand the likely impacts of ecological traps for each species.

Identifying risk areas

Based on the selected models, we generated probabilities for both live rhino and carcass occurrence in 200×200 m pixels across the study area. Following the framework established by Nielsen *et al.* (2006), we binned the resulting probabilities into 10 ordinal bins from low (1) to high (10) and used the combination of these categories to define five risk states for each rhino species: primary and secondary ecological trap, primary and secondary safe harbour and non-critical habitat (Fig. 2). We set cut-off points determined

by the data to define the boundaries between risk classes, with 90% of live rhino and 80% of carcass occurrence describing high use and high risk respectively. High use was further divided in half to represent primary and secondary occurrence. Ecological traps exhibit the highest risk for rhino, with high use and high poaching risk; these areas can be divided into primary and secondary traps in line with the probability of live rhino occurrence. Safe harbours represent the least risky areas for rhino, with high probability of use but low poaching risk; these areas can similarly be divided into primary and secondary safe harbours in line with live rhino occurrence. Non-critical habitat represents the area inhabited by less than 10% of the population.

To delineate areas for the simultaneous management of both rhino species, we overlaid and collapsed the black and white rhino risk areas into management categories: (1) threat (where both species were primary/secondary trap, or one species was primary/secondary trap and the other species was non-critical), (2) haven (where both species were primary/secondary safe harbour, or one species was primary/secondary safe harbour and the other species was non-critical), (3) species contrast (where one species was primary/secondary trap and the other was primary/secondary safe harbour) and (4) non-critical (non-critical habitat for both species). These categories were defined in terms of management actions that might be most effective. For example, both primary and secondary ecological trap areas may benefit most from increased anti-poaching actions, while both primary and secondary safe harbour areas may benefit from continued surveillance. Likewise, biological management strategies would distinguish along similar lines, with removal/rescue strategies most appropriate for the ecological trap areas, and individual-based rhino monitoring most appropriate for safe harbour areas. This combined output is therefore likely to be the most relevant for prioritizing limited resource distribution and determining anti-poaching and biological management activities by management authorities.

Results

Live rhino and carcass occurrence

Black rhino

The top-ranked model for live black rhino occurrence included all predictors except woody cover (Supporting Information Appendix S1). Black rhino occurrence decreased with increasing distance to fence for approximately 17 km, after which probability increased. Black rhino occurrence increased with distance from main rivers for the first 5 km. Occurrence and distance to roads displayed a similar relationship, with probability of black rhino occurrence increasing for the first 3 km, followed by a plateau. Conversely, as distance from human activity (ranger stations) and terrain ruggedness increased, the probability of black rhino occurrence decreased. Modelled against the Lowveld sour bushveld, black rhino showed comparative preference for mountain bushveld, Acacia thicket and Acacia savanna.

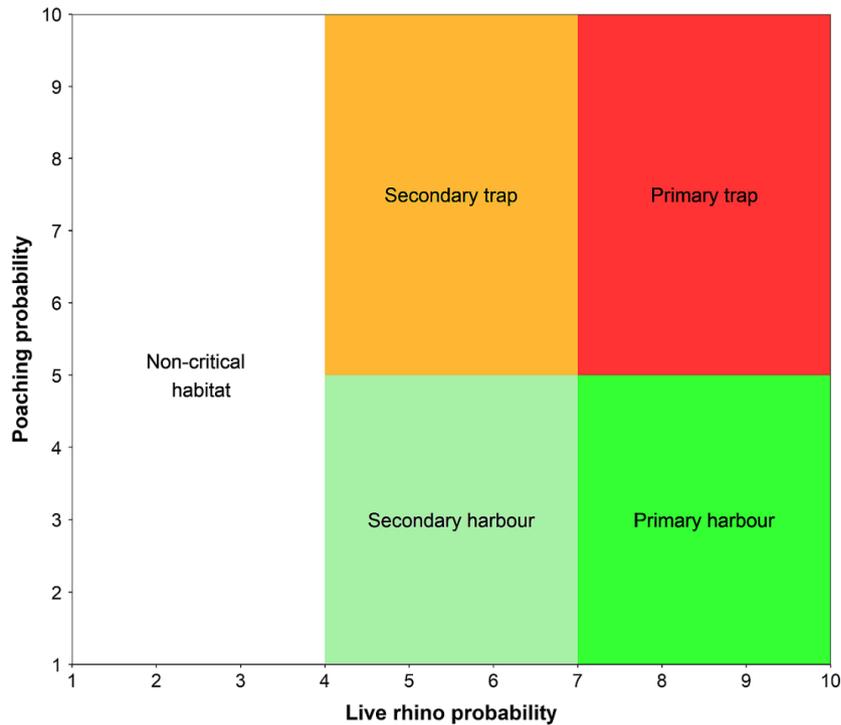


Figure 2 Example of risk states classified according to the probability of live rhino and carcass occurrence, from bin 1 (low) to 10 (high). Figure adapted from Nielsen *et al.* (2006). [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com/doi/10.1111/zsl.12111).]

Black rhino showed significant preference for Combretum woodland, mixed Combretum/Terminalia woodland, Sabie/Crocodile thicket and thornveld and significant avoidance of the Lebombo south plains.

The top-ranked model for the occurrence of black rhino carcasses included distance to fence, main rivers and roads, terrain ruggedness and woody cover (Supporting Information Appendix S1). The probability of carcass occurrence decreased with increasing distance from the fence and terrain ruggedness. Carcasses occurred more frequently closer to rivers and with increasing woody cover.

White rhino

The top-ranked model for live white rhino occurrence included all predictors (Supporting Information Appendix S1). Live white rhino occurrence increased with distance from fence for the first 10 km, then decreased steadily. Similarly, white rhino occurrence increased for approximately 7 km from main rivers, after which occurrence decreased. White rhino occurrence increased with distance to human activity and roads for an initial period (humans: 6 km; roads: 4 km) and then plateaued. White rhinos decreased with increasing terrain ruggedness, and occurred most frequently at intermediate herbaceous biomass levels. Compared to the Lowveld sour bushveld, white rhino showed significant preference for mountain bushveld, Combretum woodland, mixed Combretum/Terminalia woodland, Sabie/Crocodile thicket, Acacia savanna and thornveld and significant avoidance of Acacia thicket and Lebombo south.

The top-ranked model for the occurrence of white rhino carcasses also included all predictors (Supporting Information Appendix S1). White rhino carcass occurrence decreased with distance from fence and main rivers, but increased with distance from roads for approximately 7 km, then decreased. Carcass occurrence increased with herbaceous biomass and distance to human activity, and decreased with terrain ruggedness.

Landscape preference

The impacted and original black rhino populations showed a difference in landscape preference primarily in Acacia thicket (Fig. 3a). Small differences in Acacia savanna and Lowveld sour bushveld were seen, but these were not sufficient to change the overall interpretation of black rhino landscape preference. For Acacia thicket, however, when poached black rhino were added to the dataset, the result changed from avoidance to a neutral preference (Ivlev's index = -0.33 and 0.00 for the impacted and original black rhino populations respectively).

Comparing the impacted and original white rhino populations showed the largest difference in preference for Lowveld sour bushveld, but no differences that were sufficient to change the overall interpretation of white rhino landscape preference (Fig. 3b). Both black and white rhino showed preference for Combretum woodland, mixed Combretum/Terminalia woodland and thornveld, and avoidance of Acacia savanna, Lebombo south and Lowveld sour bushveld.

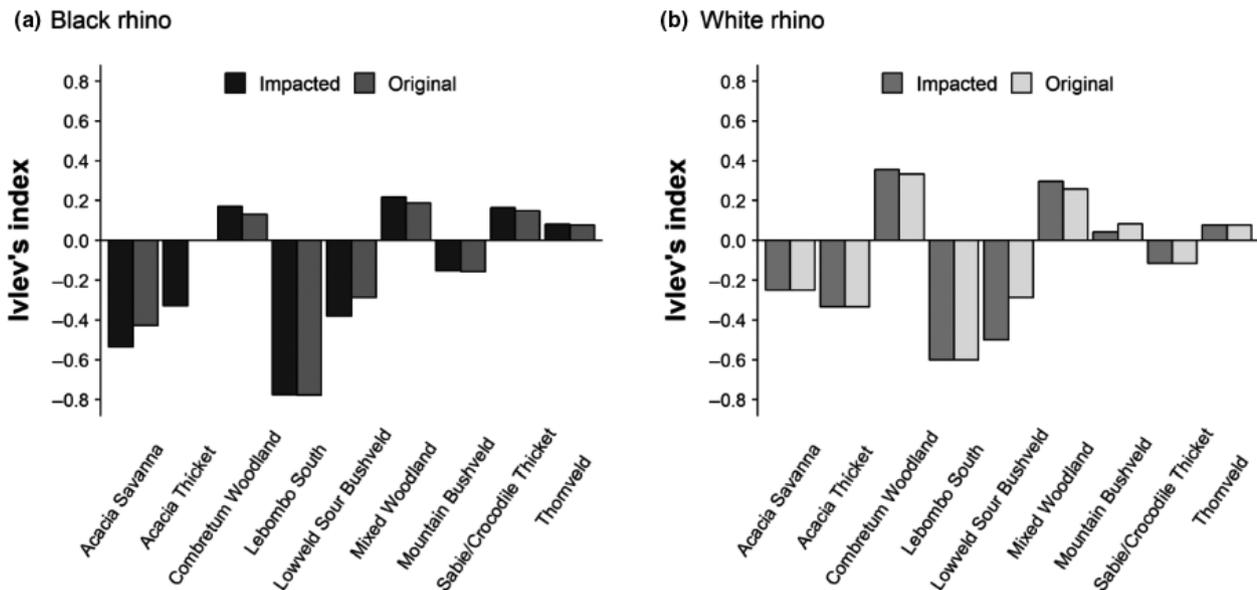


Figure 3 Landscape preference based on Ivlev's selectivity index by (a) black rhino and (b) white rhino, for the impacted and original populations.

Contrasting species preferences were shown for Sabie/Crocodile thicket (black rhino: selected, white rhino: avoided), mountain bushveld (black rhino: avoided, white rhino: selected) and Acacia thicket (black rhino: neutral, white rhino: avoided).

Identifying risk areas

Rhino occurrence and mortality probabilities were projected across the entire IPZ at 200 × 200 m resolution. Binning and overlaying these probabilities resulted in a map of risk areas in southern Kruger for each species. Black rhino showed a lower proportion of primary trap area but a higher proportion of secondary trap compared to white rhino (Table 1). Together, the ecological trap proportions were similar for both species (black: 37.73%, white: 35.51%). Black rhino showed lower proportions of both primary and secondary safe harbours than white rhino; together, the safe harbour areas were considerably lower for black rhino (black rhino: 32.01%, white rhino: 44.74%). Non-critical habitat was substantially greater for black rhino (30.27%) compared to white rhino (19.74%).

When combining and collapsing the risk areas for both rhino species into management categories, 32.48% of the IPZ were classified as threat area, 31.03% as haven, 21.21% as species contrast area and 15.28% as non-critical habitat (Fig. 4a). A high resolution, spatially explicit map is not shown for security reasons, but has been distributed to management authorities.

Discussion

The majority of covariates predicting live rhino and carcass occurrence reflected similar relationships in both analyses, suggesting that poaching risk is predominantly related to

Table 1. The area (km²) and proportion (%) represented by each risk area for black and white rhino across the Intensive Protection Zone (IPZ), Kruger National Park, predicted at 200 m × 200 m resolution

| Risk area | Area (km ²) | | Proportion of IPZ (%) | |
|------------------------|-------------------------|-------------|-----------------------|-------------|
| | Black rhino | White rhino | Black rhino | White rhino |
| Primary trap | 838.80 | 962.16 | 20.49 | 23.50 |
| Secondary trap | 705.68 | 491.80 | 17.24 | 12.01 |
| Primary safe harbour | 407.28 | 689.60 | 9.95 | 16.84 |
| Secondary safe harbour | 903.04 | 1142.24 | 22.06 | 27.90 |
| Non-critical habitat | 1239.08 | 808.08 | 30.27 | 19.74 |

ease of access in areas where rhinos are likely to be encountered in southern Kruger. Black and white rhino showed similar proportions of ecological trap, with fine-scale differences likely related to species-specific dispersal behaviour. Management categories identified approximately one third of southern Kruger as threat area. Management actions that apply interventions to different categories in accordance with their classification would be optimal for the protection of both rhino species.

Predicting live rhino and carcass occurrence

Distance to roads, terrain ruggedness, herbaceous biomass (white rhino), distance to fence and distance to rivers reflected similar relationships with live rhino and carcass occurrence. Interestingly, woody cover showed no

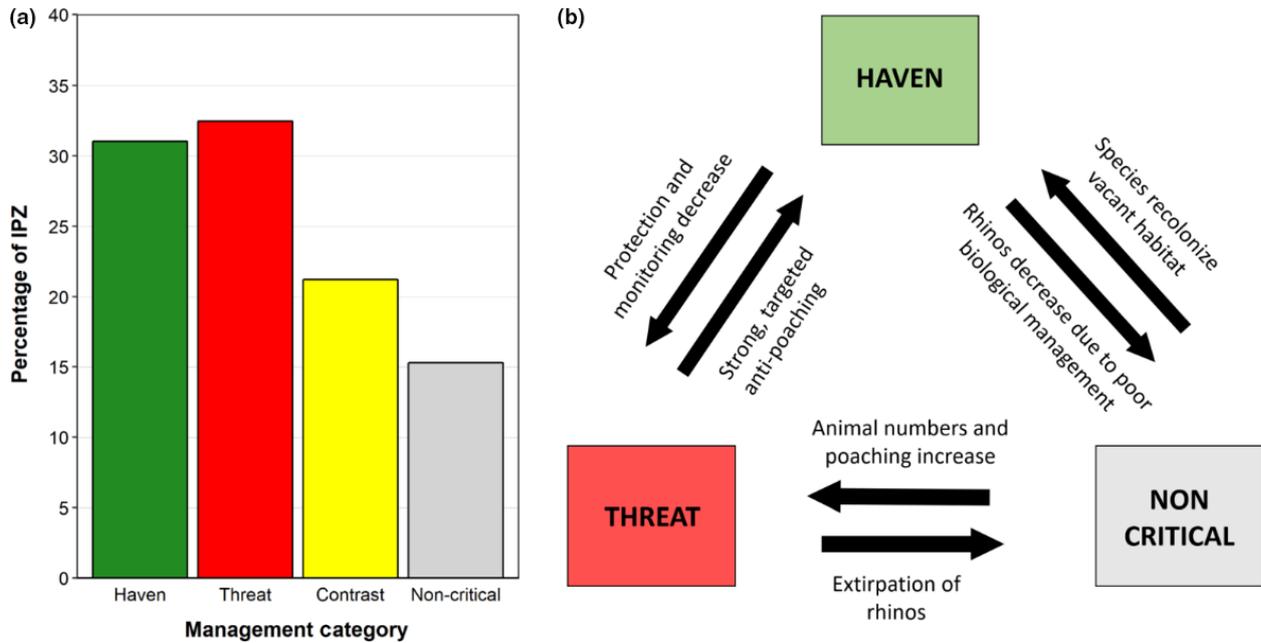


Figure 4 (a) Proportions of different management categories for both rhino species combined across the IPZ, Kruger National Park. (b) Flow chart depicting management categories and circumstances or actions that would convert one category to another. [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com).]

relationship with live black rhino but a positive relationship with poached carcasses, suggesting that poachers actively select areas with increased cover. The absence of effect on live black rhinos may be a consequence of scale, with woody cover influencing within-home range movement rather than landscape-level distribution. Live black rhino were less likely to be close to rivers, while carcasses were more likely to occur in close proximity. This may be a result of the diel behaviour of black rhino, avoiding riparian areas during the day (when the aerial census occurred) and travelling to water to drink at night (Lent & Fike, 2003). No effect of distance to human activity was seen with black rhino carcasses, but the inverse relationship was seen with live black rhino occurrence; this may reflect a correlation with another unknown habitat variable. Whether the relationship between the likelihood of being poached and the likelihood of live rhino occurrence reflects behavioural understanding by poachers or simply the greater probability of encountering rhino in particular areas cannot, unfortunately, be further elucidated in this study.

Our analyses are, however, constrained by a number of factors. The live rhino models utilized census data collected during the dry season; thus these models represent covariates predicting habitat selection specifically during the dry season. This is in contrast to the carcass data which were collected throughout the year; the carcass models thus reflect covariates influencing mortality at all times of the year. In addition, no existing water dataset fully captured all permanent surface water in southern Kruger. Main rivers are the most consistent source of water at this scale and time of year, but it is possible that additional permanent water sources

contribute to animal locations. Finally, there are likely to be potentially crucial variables influencing poacher behaviour and movement, such as the locations of permanent or temporary access points and insider information regarding capture risk in different areas, which could not be incorporated. The main purpose of this work, however, was to provide the best predictive power with the data that were available.

Risk areas and dispersal behaviour

Ecological traps occur as a result of distorted cues of habitat quality, a change in habitat quality despite the presence of the original cues or a combination of both methods (Robertson & Hutto, 2006). We propose that areas that exhibit both high probability of rhino occurrence and high mortality risk function as ecological traps, as these areas convey reduced survival probability as a result of poaching. Furthermore, the cues of habitat quality may also be distorted as high-quality habitat with low rhino density likely to exhibit increased attractiveness for individual dispersal. Differences seen in the proportions of risk areas between black and white rhino may be partly a consequence of species-specific dispersal behaviour rather than ecological specificity or poaching susceptibility. Black rhino are known to be poor dispersers and may take long periods of time to colonize or recolonize vacant habitat (Linklater & Hutcherson, 2010). Thus following the large-scale removal of animals within a particular area, it may take some time (or incentive) for black rhino to move back into the area. White rhino, however, often move large distances into unoccupied or low-density areas (Norman Owen-Smith, 1983).

The lower numbers of black rhino combined with poor recolonization of empty habitat would result in primary traps converting to secondary traps (as some black rhinos are removed by poaching) and then to non-critical habitat (as most or all are removed by poaching) far more readily than for white rhino. This is reflected in the comparative statistics for these risk areas: primary trap proportions are lower for black rhino than white rhino, secondary traps are higher and non-critical areas are higher still. If poaching remains localized for a substantial time period, however, the poor recolonization behaviour of black rhino may, in fact, confer a 'protective' effect of sorts; once poaching has extirpated a local population, there are simply no remaining black rhino to poach within that area. White rhino, however, would not enjoy the same protection. Continued movement and dispersal into vacant habitat would perpetuate the cycle and ecological trap areas would continue to function as population sinks (Pulliam & Danielson, 1991) for white rhino. This behaviour is, in fact, actively utilized by park authorities in other reserves for white rhino population management (Owen-Smith & Shrader, 2002). If this is the case, black rhino may experience less severe consequences from ecological traps than white rhino.

The 'avoidance' of Acacia thicket by the impacted black rhino population and 'neutral preference' of the original population support the local extirpation and poor recolonization hypothesis. The Acacia thicket landscape represents the smallest physical area of the nine IPZ landscape types, and hosted the highest number of poached black rhino carcasses per unit area over the study period (data not shown). The extent of the selectivity change is also likely to be under-representative, as each carcass was included only once in the original population dataset, while there would likely be multiple sightings of individual live rhino over the 5-year period. The population size of black rhino in southern Kruger is most likely below the level at which density-dependent social pressures would increase dispersal; this may have resulted in this landscape remaining vacant even if it was a preferred type. Alternatively, the high mortality per unit area may be perceived by black rhino as dangerous, reducing the quality of that landscape and resulting in active avoidance. While bolder or more aggressive animals typically need stronger cues to avoid danger (Robertson *et al.*, 2013), the high mortality per unit area in the Acacia thicket may be sufficient to be perceived as such by black rhino.

The probability of extinction of a population as a result of an ecological trap increases with the severity of the trap and the fraction of the population that is trapped (Robertson, Rehage, & Sih, 2013). The severity of a trap for a particular species is often determined by the type of population sink that the ecological trap represents (Robertson, Rehage, & Sih, 2013). A severe trap is more attractive than other habitats and draws animals in, thus perpetuating the cycle, while an equal-preference trap exhibits the same draw as other areas, and typically has less severe consequences for the population (Robertson *et al.*, 2006). Identifying the type of trap experienced by black and white rhino is therefore

relevant to the long-term prognosis for each species. Susceptibility to traps can also be related to specific age and sex classes (Robertson *et al.*, 2013); for example, young dispersing males may be drawn into a trap area due to a lower density of dominant bulls (severe trap), but other classes may exhibit a neutral preference for the trap area (equal-preference trap). The results of this study suggest that ecological traps within Kruger may act more as equal-preference traps for black rhino (particularly while the population remains at low density) and severe traps for white rhino; future work identifying whether these designations are specific to particular age/sex classes would be beneficial for individual species predictions and management.

Management implications

Collapsed management categories for black and white rhino resulted in 32.58% threat, 31.03% haven, 21.21% species contrast and 15.28% non-critical habitat. Grouping both species' primary and secondary ecological traps into one 'threat' category, and both primary and secondary safe harbours into one 'haven' category is a relatively crude approach, but one that enabled the simple classification of just four categories that are likely to benefit from different management actions. We surmise that this type of output is the most practical and likely to be implemented by conservation authorities. Management interventions that (1) convert threat areas and non-critical habitat (where possible) to havens, and (2) maintain current havens, would likely make the best contribution to rhino protection in southern Kruger with limited capacity and resources (Fig. 4b). These may include heavy anti-poaching interventions in threat areas, increased rhino monitoring and biological management in havens and possibly animal translocations back into non-critical habitat under specific circumstances. Noteworthy is the absence of havens around the Kruger boundary; the area adjacent to the fence is almost entirely threat, species contrast or non-critical area. This suggests that poachers are still predominantly operating in easily accessible areas and that increased focus on access points, fence improvements and boundary protection is still likely to be highly effective.

Conclusion

Black and white rhinos are under severe poaching pressure in South Africa, which threatens them at the local population and species level. Until the illegal demand for rhino horn decreases, active protection in the form of anti-poaching and optimal biological management to recover populations will continue to be crucial for species survival. We classified the IPZ, a high-priority area in southern Kruger, into management categories that reflect the actions most likely to be effective for rhino protection in those areas. The IPZ comprised 32.58% threat, 31.03% haven, 21.21% species contrast and 15.58% non-critical habitat. For protected areas, the size of Kruger, prioritized distribution of resources and manpower are needed, as it is impossible to uniformly cover such an expanse at the intensity level that is currently

required. Management actions associated with converting threat areas to havens and maintaining the current havens would provide optimal protection for both rhino species simultaneously with limited resources. This work illustrates how the conservation of multiple species or taxa within a system can be simultaneously prioritized in vast areas where resources and/or capacity are insufficient to undertake species-specific approaches.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Top-supported resource selection functions for live rhino and carcass occurrence.