Exploring drivers of human tolerance towards predators

A case study on tolerance on private farms in rural northern South-Africa

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Abstract

Carnivore populations are declining worldwide, with the main drivers being habitat loss, degradation and poaching. In many regions expanding human populations and increasing competition with humans for natural resources are putting rising pressures on carnivore populations. Especially in Africa, where rapid land use change, habitat degradation, habitat fragmentation and increasing human-wildlife conflict play a growing role in population declines for many large carnivores. Retaliatory killings as a result of human-wildlife conflict are believed to have significant effects on predator extinction risk outside of protected areas. Tolerance-based conservation methods such as implementation of financial and communal incentives have been proven to be effective in reducing retaliatory killings of large carnivores. To be able to apply these conservation methods it is important to understand how tolerance is shaped locally. This study aimed to identify possible important factors that shape tolerance in northern South Africa using surveys on private farms and camera-trapping data. Significant negative correlations were found between tolerance levels and perceived conflict, livestock farms and perceived predator presence. A significant positive correlation was found between tolerance levels and game farm sizes. The absence of a correlation between most observed predator presences and tolerance level suggests that tolerance is not generally shaped by

actual predator presence. These findings back the idea that tolerance targeted conservation may be more effective and beneficial for both community and predator livelihood than conservation strategies targeting predators like predator removals.

Introduction

Worldwide carnivore populations and available home ranges are declining, as a result of human-induced habitat loss, degradation and overexploitation in the form of poaching (Wolf & Ripple, 2017; WWF, 2024). Africa, the continent with the most functionally diverse carnivore guild, is experiencing significant population declines, with species like cheetah (*Acinonyx jubatus*), lion (*Panthera leo*) and African wild dog (*Lycaon pictus*) facing extinction outside of protected areas (PAs; Bodasing, 2022). The use of PAs is a common conservation practice with the goal to reduce human impact, protect local biodiversity and maintain ecosystem services (Watson et al., 2014). Cheetah (*Acinonyx jubatus*) for example, are protection-reliant species, meaning that they rely on these PAs to sustain their populations. However, approximately 77% of their current range is outside of these PAs (Durant et al., 2017). Protection-reliant species are often subject to systematic underestimation of extinction risk due to lack of information outside of PAs (Durant et al., 2017). The focus on PAs in conservation practices therefore limits conservation efforts for species with ranges that stretch beyond these areas. (Durant et al., 2017; Williams et al., 2022).

In these non-PAs the extinction risk can be substantially higher due to human-wildlife conflict (Seoraj-Pillai & Pillay, 2017). Africa has the highest amount of human-carnivore conflict studies worldwide with conflict continuously increasing across many parts of the continent as a result of large overlaps between decreasing geographic distributions of carnivores and expanding farming land-use (Bodasing, 2022; Seoraj-Pillai & Pillay, 2017). As a result of this conflict many mesopredators (1kg - 15kg) and large carnivores (>15kg) are being poached as a form of retaliation, increasing survival pressures on carnivore populations (Bodasing, 2022; Buskirk, 1999; Ripple et al., 2014). Various studies have shown that human-wildlife conflict is highest in areas bordering PAs due to (perceived) poor fencing management (Pekor et al., 2019; Seoraj-Pillai & Pillay, 2017; Soliku & Schraml, 2018). Outside PAs, human-wildlife conflict with large predators can result in retaliatory killing, even when the actual impact of predation is relatively minor in comparison to the impacts of for example disease and weather effects on people’s livelihoods (Kissui, 2008; Mare et al., 2018; Viollaz et al., 2021).

The cause of retaliation is more frequently related to societal and behavioral factors such as the lack of governmental support and mistrust or fear for wildlife, but also social and cultural factors are often significant drivers (Dickman et al., 2014; Gálvez et al., 2021; Marchini & Macdonald, 2012; Prokop et al., 2009; Viollaz et al., 2021). These social and cultural factors are important in shaping people's tolerance towards predators. Tolerance as defined by Frank (2016) is the acceptance towards feelings, habits, beliefs, or behaviors differing from or conflicting with one’s own. In the context of this study it is the willingness of humans to accept predator presence even if these predators are conflicting with their own interests.

The integration of these social and cultural factors into conservation practice through tolerance-focused approaches has been an increasing topic over the last decades, especially since conflict itself is not always an accurate predictor of people's tolerance towards predators (Lischka et al., 2019). Conservation studies aimed at increasing local tolerance towards predators have been proven to be effective in decreasing retaliatory killing of predators (Hazzah et al., 2014; Zabel & Holm‐Müller, 2008). In the study of Hazzah (2014), local tolerance in Maasailand, Kenya was enhanced by providing financial support to compensate for livestock losses caused by large carnivores and through community aimed incentives like education,

conservation-related employment and community assistance all which were directly linked to lion presence.
To be able to effectively apply tolerance-based strategies it is important to understand how tolerance is shaped and influenced locally. Therefore it is important to understand how tolerance may be affected by human perception, presence of predators and other possibly relevant factors like land-use. South-Africa provides a study setting where the ranges of mesopredators and large carnivores overlap with areas of high conflict risk, regions outside of PAs where human-carnivore competition is high and predators face elevated probabilities of persecution, as mapped by Ripple et al. (2014). This study aims to identify the key factors affecting tolerance towards meso- and large predators in rural northern South-Africa. Northern South-Africa is dominated by private and communal farms and largely overlaps with the ranges of most of South-Africa's mesopredators and large carnivores like cheetah, leopard (*Panthera pardus*), brown hyena (*Hyaena brunnea*) and spotted hyena (*Crocuta crocuta*) (ESRI, 2021; Ripple et al., 2014; IUCN, 2025; Thorn et al., 2011). Human-wildlife conflict is commonly studied across northern South-Africa (Seoraj-Pillai & Pillay, 2017).
I hypothesize based on recent studies (Kansky, 2015; Kansky et al., 2016; Viollaz et al., 2021) that perceived conflict may not be an accurate indicator of tolerance, and can only partially explain decreases in tolerance with increasing perceived conflict. Instead, I expect differences in tolerance between land-use types, as damages due to predation is more likely in livestock and game farms than in agricultural farms (Du Plessis et al., 2018; Marchini & Macdonald, 2012; Pirie et al., 2017). Additionally, I expect a negative correlation between the presence of predators and tolerance.
Understanding how tolerance is shaped is important for effective implementation of tolerance-based conservation strategies and can be a way to reduce extinction risk of predators outside of PAs. Locally, tolerance-based conservation can reduce pressures on the livelihood of farmers and positively aid social and economical development, similar to the results of Hazzah (2014) and Zabel & Holm-müller (2008) where both social and financial incentives aided local communities and predator conservation.

Research question

What factors are associated with local tolerance towards predators in rural northern South Africa and how do they correlate?

Methods

The data used for this study was collected as part of the free-roaming cheetah census (FRCC), a joint venture between Ashia Cheetah Conservation NPC, Cheetah Outreach Trust, the University of Groningen and, until end of 2024, Stellenbosch University. This study was allowed to make use of approx. 70% of the complete FRCC database. FRCC was conceptualized, managed and almost fully funded by Ashia Cheetah Conservation. Data collection used in this research, in the form of farmer questionnaires, scat and DNA collection, movement data and camera-trapping, was targeted at the cheetah (A. jubatus), but also included other predators from the canidae, hyaenidae and felidae families in the study area. No invasive methods were used to obtain data in this study. The FRCC was conducted under the following ethical permits obtained from Stellenbosch University: Animal Care and Use (ACU-2024-28260) and Social, Behavioural, and Educational Research (SBER-2024-24927). The data is licensed by Ashia Cheetah Conservation NPC as creator under the Creative Commons Attribution-No Derivatives 4.0 International license (CC BY-ND 4.0 International). This license requires that reusers of the FRCC data or part thereof give credit to the creator. It allows reusers to copy and distribute the material in any medium or format in unadapted form only, even for commercial purposes. For this case study, Ashia (for contact www.ashia.co.za) allowed the author to remix and adapt some of the FRCC data.

Study area

The study area comprises an area of approximately 95.500km^2 along the northern border of South Africa, in the provinces Northern Cape, North West and Limpopo (Figure 1). Since data was collected by the field teams of the FRCC, which is focused on the African cheetah, the study area follows the cheetah IUCN range for South Africa. Urban areas and PAs (e.g. Kruger National Park and the Kgalagadi) are excluded from the study area. The study area contains an approximate of 17.000 private and communal farms, which covers 96% of the study area (ESRI, 2021). The study area is divided into quarter degree grid cells (QDGC) of 25km^2.
The target predator species for this study are cheetah, leopard, caracal (*Caracal caracal*), African wildcat (*Felis lybica*) , serval (*Leptailurus serval*), black-backed jackal (*Lupulella mesomelas*), brown hyena, spotted hyena and African wild dog (*Lycaon pictus*). All which can be found within the range of the study area according to their IUCN ranges (IUCN, 2025). Lions are excluded from this study as they are no longer free-roaming across South Africa.
The climate across the entire study area is semi-arid to arid (Loarie et al., 2009) and consists of forested areas, grasslands, shrublands, cultivated lands and deserts (Shikwambana et al., 2023). Fencing of the private lands in the study area can result in severe fragmentation of the landscape when the fencing (mostly) consists of predatory proof fences and remain well maintained, as carnivores and other wildlife require fence holes to allow crossing (Pirie et al., 2017). The result of this high fragmentation is an increase in human-wildlife conflict due to competition for resources like food, space and water in the study area (Seoraj-Pillai & Pillay,

2017).

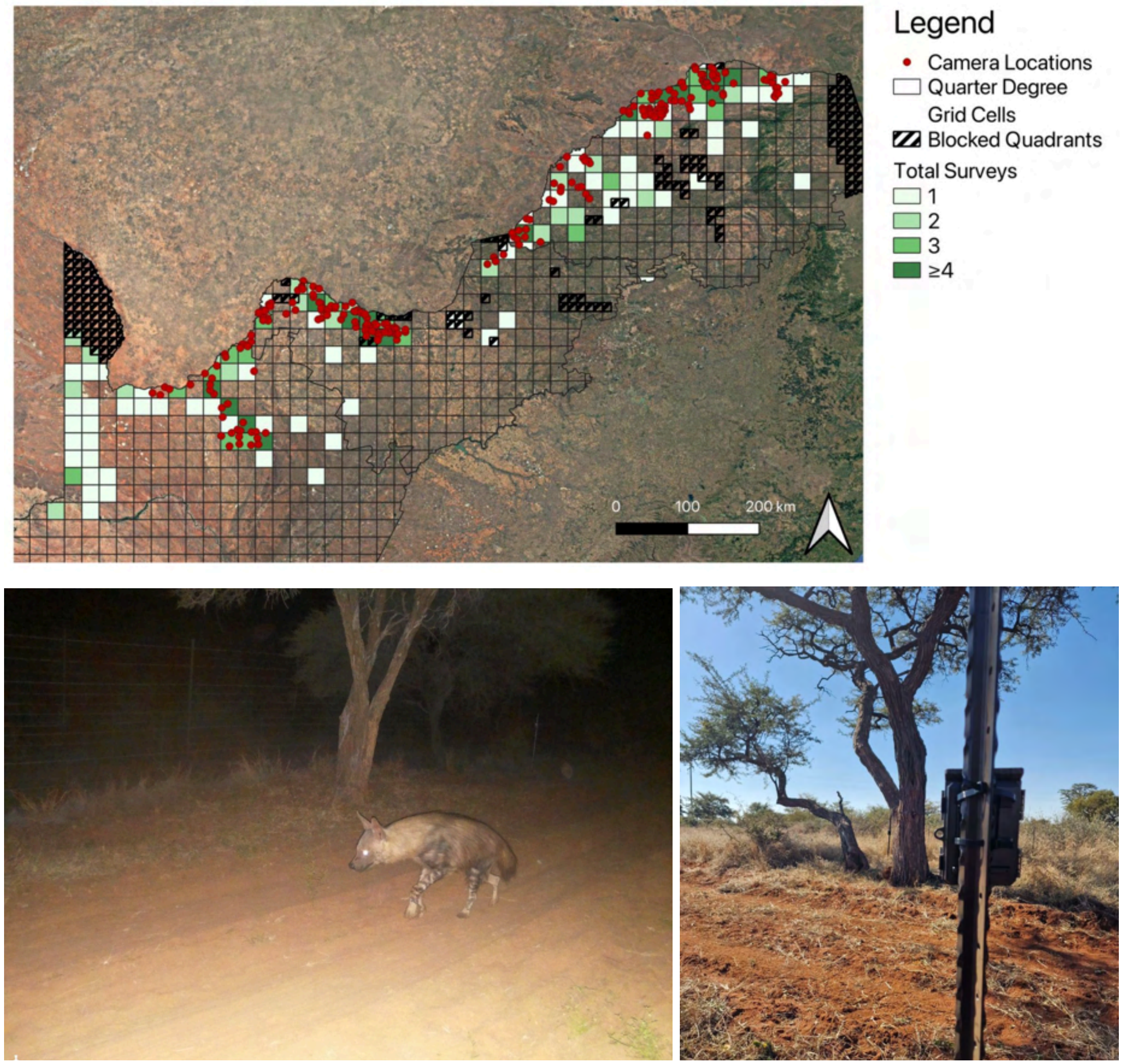


Figure 1A-B. Map of the study area (A;top). QDGC overlay across provinces Northern Cape, North West and Limpopo (left-right). The amount of surveys per grid cell are shown by the color scale up to the sampling goal of 4 surveys per grid and camera locations are indicated by the red dots. Blocked quadrants indicate areas that are excluded from the study area because they contain PAs, urban areas or are otherwise inaccessible due to safety risks. Images of sentinel sites and camera setup (B;bottom). Sentinel site images show trails along fence lines including a playtree (right).

Data collection

Survey

Landowners and managers of private farms and game areas were surveyed across the study area within a 28-month time period from September 2022 to December 2024 as part of the FRCC that runs until December 2025. Surveys were developed in KoboToolbox and conducted in person, over telephone or online. To ensure systematic data collection, the QDGCs were used, with cell sizes adjusted for borders, cities, and inaccessible areas. Minimum survey targets were set by cell size: four surveys for full cells, three for two-thirds, two for half, and one for smaller cells (Figure 1A). A total of 293 surveys were conducted across 137 grid cells. The survey consisted of 329 questions ranging from general information on the farms, animals on the private lands and on tolerance and perception towards animals.
To assess the tolerance level of landowners 4 Likert scale survey questions on tolerance towards predators on their land were used (Appendix A). The answers were converted to a numerical scale with 5 levels corresponding to the 5 levels of the Likert scaled answers, each level being considered as relatively equal steps. The numerical values of the 4 questions were summed up to form the tolerance level.
Questions on the perceived presence of free-roaming predators could be answered with never, rarely (approximately once a month) or often (approximately once per week). Perceived conflict questions could be answered by the frequency of which conflict takes place (seasonally;1/4,monthly;1/12,weekly;1/52, daily;1/365) and which predators are causing the conflict. Land-use questions were answered based on the proportion of land-use type present at a farm. Questions on guard dogs were answered as to the absence or presence of guard dogs on the private lands.

Camera trap

For the camera trap placement the QDGC were divided in four quadrants of 12.5x12.5km. Camera traps were placed in the quadrants to ensure that ¾ of the quadrants were occupied by a camera site. Camera traps were placed in the quadrants using a standardized protocol (Appendix B). Sites were selected within these quadrants (Figure 1A) at areas called sentinel sites. Sentinel sites consist of sites with points of interest eg. play trees, fence lines, waterholes or animal crossings (Figure 1B); these factors contribute to the likelihood of observing predators. Each sentinel site has 2 active cameras both facing the point of interest, but not directly each other to increase the angle of observation without a glare from the camera flashes (Figure 2). The distance between the camera and the point of interest ranges from 7-10 meters. Cameras were checked regularly (approximately every 6 weeks) in order to prevent data loss. All camera images were uploaded to TrapTagger (WildEye, 2025) and annotated. Annotation was done by both AI and humans. In cases where AI could not certainly annotate species, human annotation was done. All predator sightings were manually checked and counted. All images in a 30 minute time interval were clustered, meaning that images that occurred within 30 minutes are considered a single observation to reduce non-independent observations, following commonly used camera-trapping protocols (Wearn & Glover-Kapfer, 2017).

In total 3 million+ images were collected between September 2022 and December 2024. To maximize the spatial overlap between surveys and camera-trapping sites, all images from this period were used, even when they fell outside of the survey sampling period. Overall, 26.535 images contained predators, grouped in 7.200 individual clusters across 69 grid cells. The total trapping effort was 59.875 unique trapnights across the entire study period, 1 trapnight is a single active night at a sentinel site per paired camera even if 1 camera is disabled. The average trapnights per grid cell is 907,4 trapnights and the median is 635 trapnights. The lowest trapnights in a grid cell is 48 trapnights and the highest is 3192 trapnights.
To account for differences in trapping efforts observations were standardized by the trapping effort per site and a minimum trapping effort threshold of 100 trapnights per grid cell was set based on a report by Wearn & Glover-Kapfer (2017). The relatively low threshold was chosen as with low trapping effort it is still possible to detect species with high local abundances and unlike sites with very low (<100 trapnights) trapping efforts it is less likely to inflate standardized observations and make them unreliable for analyses. Furthermore, the goal of these analyses is to examine correlations between presence and relative abundance with tolerance, rather than to estimate or compare species abundance across sites directly, which would require higher trapping efforts and extremely careful analyses in order to obtain reliable results (Sollmann et al., 2013; Wearn & Glover-Kapfer, 2017). Two sites corresponding to 2 surveys were excluded because the trapping effort threshold was not met. These low-effort sites showed disproportionately high observation rates, indicating that the standardized observations were likely inaccurate under low trapping effort.

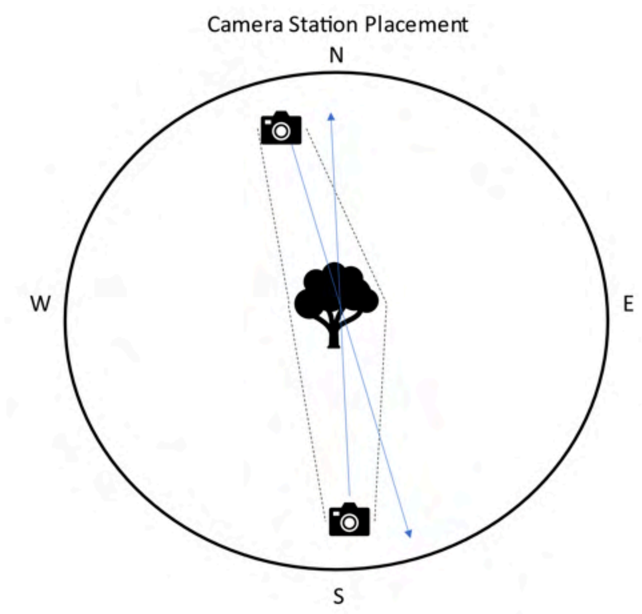


Figure 2. Camera placement at sentinel sites. Distance between cameras and points of interest range from 7-10 meters. Cameras are placed at a slight angle to prevent activation by the opposing camera's flash.

Analysis

All data analyses were performed in R version 4.4.2 (R Core Team, 2024). The tolerance level was treated as a continuous variable for the analysis (Sullivan & Artino, 2013). The resulting tolerance levels range from -2 (least tolerant) to 2 (most tolerant) in steps of 0.25.
The analysis was limited to a subset (n=161) of the complete dataset, to allow for mixed effects modelling to handle non-independent samples. Only surveys from respondents who reported being impacted by human–wildlife conflict were included in the subset. Differences in tolerance level between the subset and the remaining dataset was tested using a t-test. Differences between provinces were tested on both the full dataset and the subset using a Kruskal-Wallis test and One-way ANOVA respectively.
To test for possible relationships between tolerance level and multiple variables, Linear Mixed Models were used from the package 'lme4' (Bates et al., 2015) to account for random effects. Explanatory variables that were tested for using LMM include land-use type, perceived predator presence, perceived predator conflict, observed predator presence, predator composition and presence of guard dogs.
The mean area (ha) of land-use type per grid cell was calculated using the proportion of land-use indicated in the surveys multiplied by the total farm size of the respondents. Land-use types were tested separately and together in LMMs as they are not mutually exclusive. The land-use types were also tested on absence/presence of the land-use type.
For the analysis using the observed predator presence all clusters were standardized by the trapping effort at their corresponding sentinel sites. In total the observations of 43 grid cells correspond to 93 surveys in these same grid cells, 2 of these grid cells and surveys were excluded as they did not meet the trapping effort threshold. The remaining 44 surveys had no camera traps in their corresponding grid cells. The stability of predator compositions per grid over the years was tested with a PERMANOVA using a Bray-Curtis dissimilarity matrix using the adonis2() function from 'vegan' (Oksanen et al., 2025). Permutations were limited to only within grid cells to effectively test for any significant differences in predator composition between years. PERMANOVA was also used to test the effects of trapping effort and amount of sentinel sites on predator observations to validate the use of standardized predator observations for the analyses.
To test for correlations between tolerance level and species composition, a 3-dimension NMDS was performed on the observed species presence data including only trapping data in grid cells corresponding to the survey grids. The 3 NMDS axes were used as explanatory variables for species composition and visualized in NMDS plots including visual grouping for provinces and arrows to indicate the effect per predator species.

Results

Distribution, land-use and guard dogs

The t-test between the subset of the data and remaining data showed a significant difference (Figure 3). The subset of the data, consisting only of respondents with reported conflict, has a lower average tolerance-level at 0.26 while the remaining dataset without conflict responses has an average tolerance level of 0.60 (p<0.001).

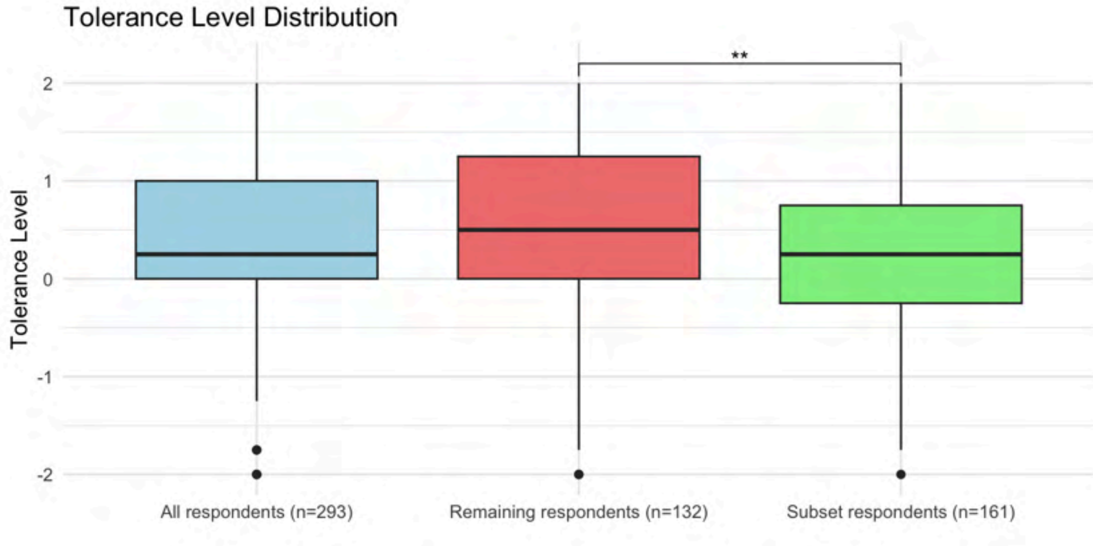
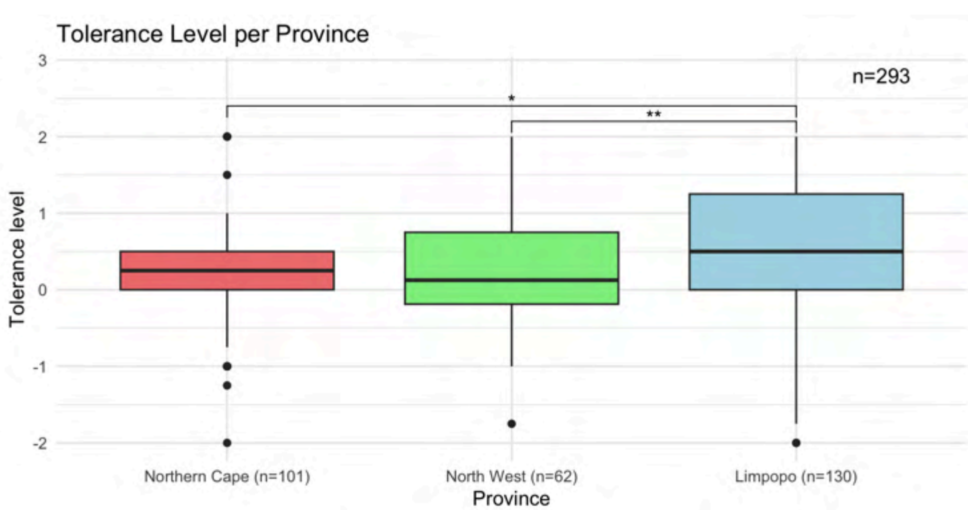
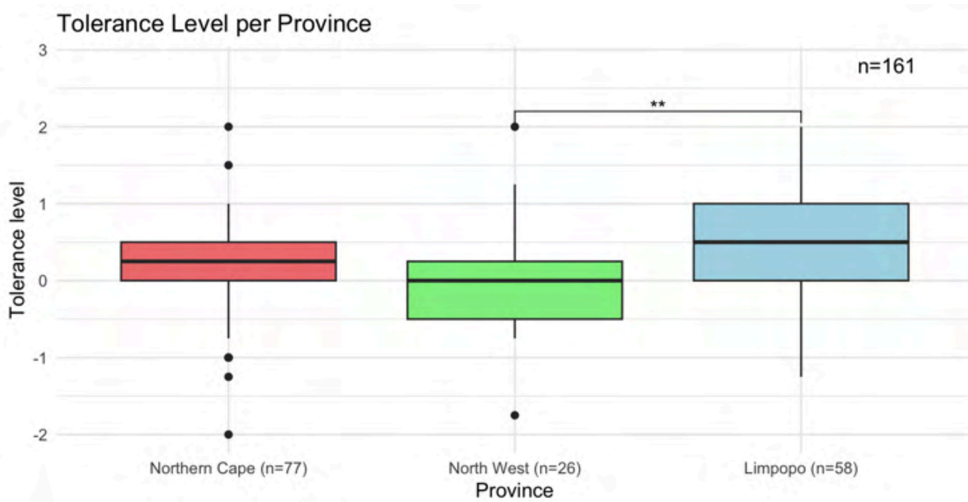


Figure 3. Distribution of tolerance levels across the full dataset, subset of the data and the remaining data. N indicates the number of surveys. (**=p<0.01)

A Kruskal-Wallis test on the complete dataset shows that there is significant difference in tolerance level between provinces in the full dataset (p=0.002). Using a pairwise Wilcoxon test, adjusted for multiple comparisons, as post hoc, it shows that both the North West province and Northern Cape province have a significantly lower mean than the tolerance level of the Limpopo province with p-values of 0.0023 and 0.0202 respectively (Figure 4A). A One-way ANOVA on the subset shows that there are only significant differences in tolerance level between the Limpopo province and North West province, the average tolerance level in North West is 0.53 lower than in Limpopo (p=0.007) (Figure 4B).





Figures 4A-B. Tolerance distribution between provinces for full dataset (A;top) and subset of the data (B;bottom). N indicates the number of surveys. (*=p<0.05; **=p<0.01)

A simple LMM with only the grid cell as a (random) factor indicates that about 45% of the variance in the dataset is a result of variation between grid cells. LMM for absence/presence for the different land-use types show significant results for the livestock land-use type (Figure 5). In a model including only livestock as a fixed predictor, the presence of livestock correlates with a decrease of 0.38 in tolerance level (p=0.004). There were no significant differences in tolerance level for the absence or presence for the other land use types.

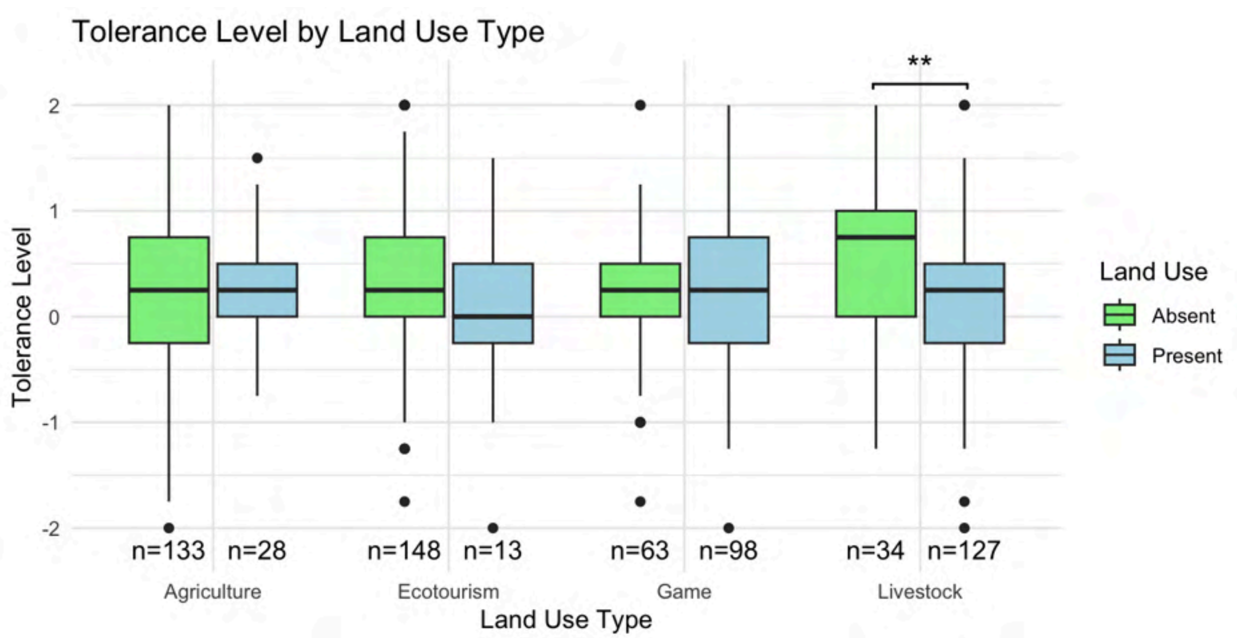


Figure 5. Distribution of tolerance level per absence/presence by land use types. N indicates the number of surveys. (**=p<0.01)

The LMMs for average land-use type allocated per grid cell (ha) individually show no significant effects for agriculture, livestock and ecotourism. Larger mean game areas per grid cell correlate

with significantly higher tolerance levels (p=0.005) at slope of 0.040 per 1000 hectares (Appendix C1). When combining all the land-use types in a single LMM it shows significant results for livestock and game area sizes. Larger game areas again correlate with a significantly higher tolerance level (p<0.001) and larger livestock areas correlate with a significantly lower tolerance level (p=0.009). The corresponding slopes are 0.053 and -0.038 per 1000 hectares, respectively (Appendix C2). Additionally there seems to be no significant effect of the cumulative farm size of the respondents per grid cell on tolerance level. The variation in tolerance level of the data explained by the fixed effects in the land-use models is between 5% and 11%.
LMMs for the absence or presence of guard dogs showed no significant correlation with tolerance levels.

Predator observations and composition

All target species were observed during the study period. Observations from 43 grid cells corresponded to a total of 93 surveys. The remaining surveys had no camera traps corresponding to their grid cells. The least observed target species was the wild dog (4 clusters) and the most observed target species was the black-backed jackal (3402 clusters) for the grid cells that have corresponding surveys. The amount of observations for all the species are shown in Table 1. Table 1 shows that the standard deviation is relatively high for most species suggesting that observations are unevenly distributed across grid cells.

Table 1. Camera trap observations (i.e. images) per species, including total observations and mean, standard deviation and median observations per grid cell for non-zero observation grid cells. The table only includes grid cells (n=41) corresponding to surveys.

Species	Total observations (images)	Mean observations per grid cell	Standard deviation per grid cell	Median observations per grid cell	Number of grid cells with observations
Black-backed jackal	3402	87.2	121.7	35.0	39
Cheetah	904	69.5	82.3	53.0	13
Brown hyena	526	15.9	14.9	16.0	33
Leopard	220	9.2	11.4	4.5	24
Caracal	194	6.7	7.5	4.0	29
Wildcat	181	6.0	6.2	4.5	30
Spotted hyena	61	8.7	9.8	2.0	7

Serval	16	2.7	1.9	2.5	6
Wild dog	4	2.0	1.4	2.0	2

Most observations were made in the Limpopo and North West provinces and the least in Northern Cape. The total trapping effort shows a similar pattern. The PERMANOVA with permutations restricted to within grid cells, to account for repeated measurements within grid cells, show that there is no significant difference in predator composition between the sampling years. Additionally, the same test using trapping effort as explanatory variables show that trapping effort significantly affects the predator composition. This validates the standardization of the predator observations by trapping effort. The sum of standardized observations of each grid cell per province ranges from 2.91 to 3.93 (Figure 6).

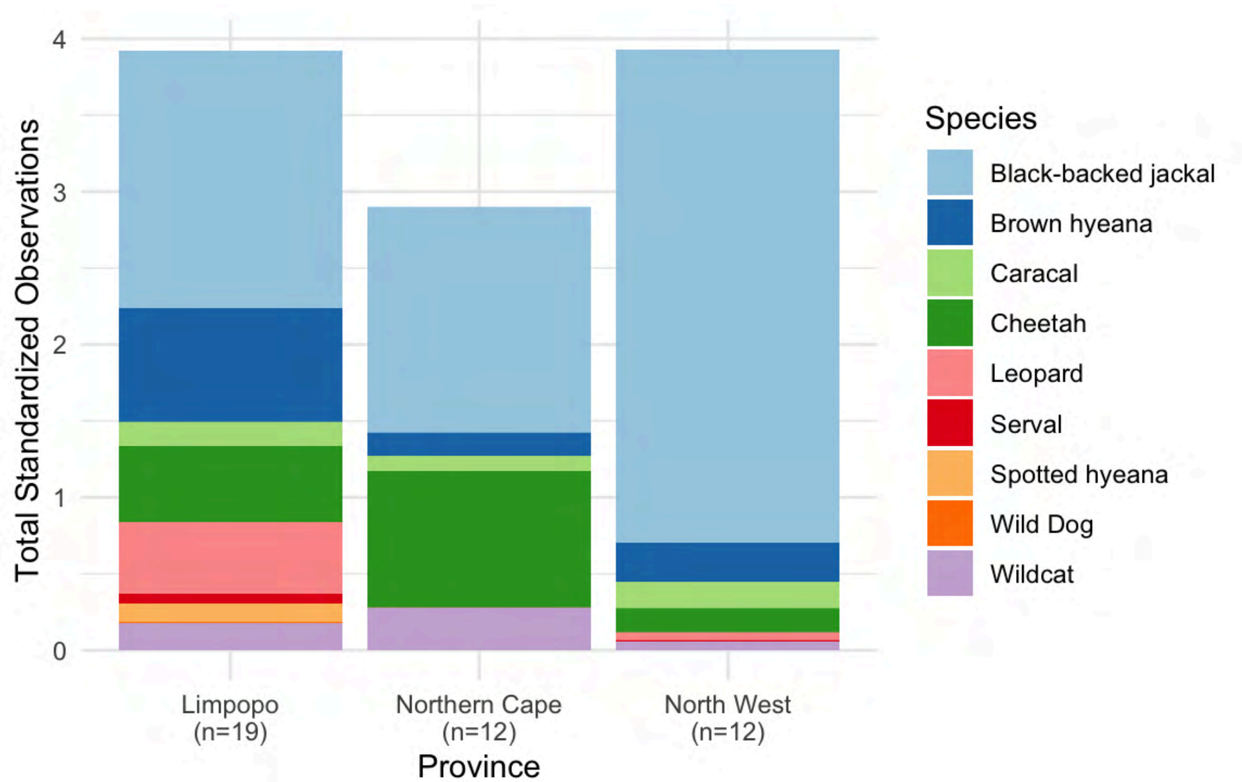
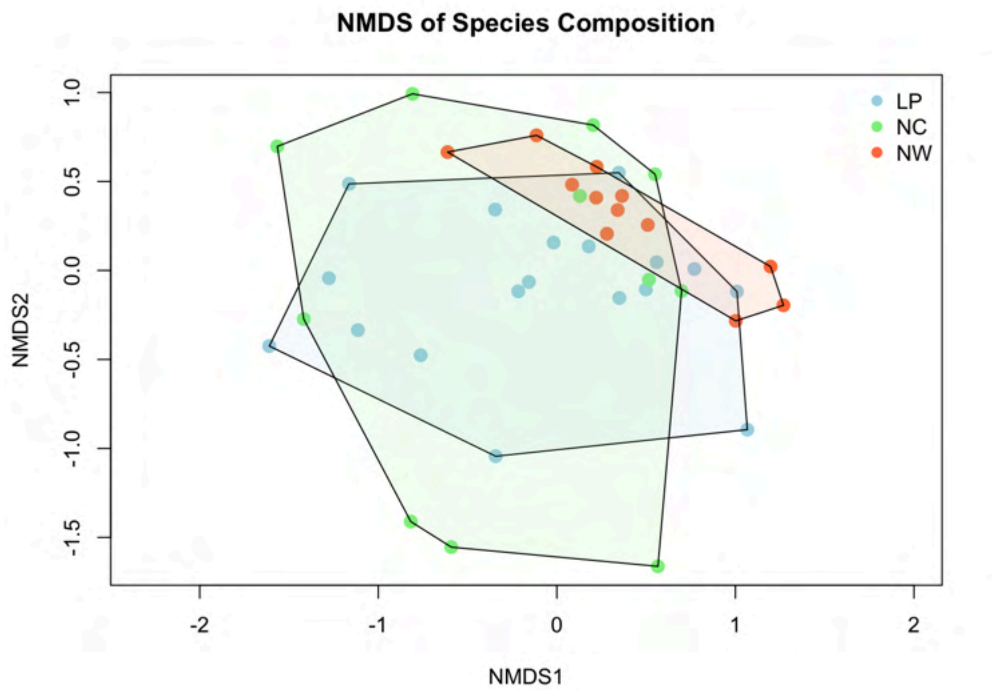


Figure 6. Standardized observations per grid summarized per province n indicates the number of grid cells per province. The figure includes only grid cells with corresponding surveys. (n=43)

PERMANOVA testing for the effect of the amount of sentinel sites on the predator composition shows that the amount of sentinel sites may only have little effect (R^2=0.03) at a marginally non-significant p of 0.072 in this dataset.
The NMDS plot (figure 7A) shows that there is less variation within the province in species composition in North West than in Limpopo and Northern Cape. The polygons of both Limpopo and Northern Cape largely overlap, most of the overlap is related to overlapping lower predator observations which can be seen by the predator arrows indicating higher densities on the other side of the plot, which the highest variation coming from the black-backed jackal and African

wildcat observations (figure 7B). When performing a LMM for the relationship between tolerance levels and the NMDS axes as a proxy for species composition it does not show any significant results.
LMM of the observed species presence for caracals show a significant (p=0.02) negative correlation between caracal presence and tolerance levels, the model explains approximately 11% of the variation in tolerance levels (Appendix D). No correlations were found between species richness, total observations or other individual species observations and tolerance level.



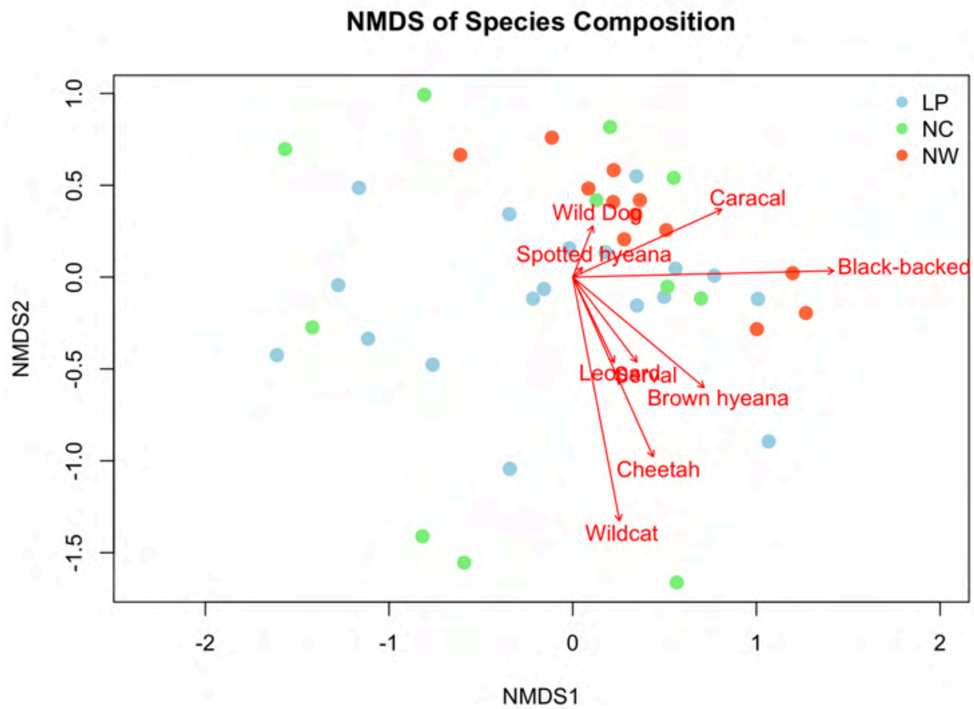
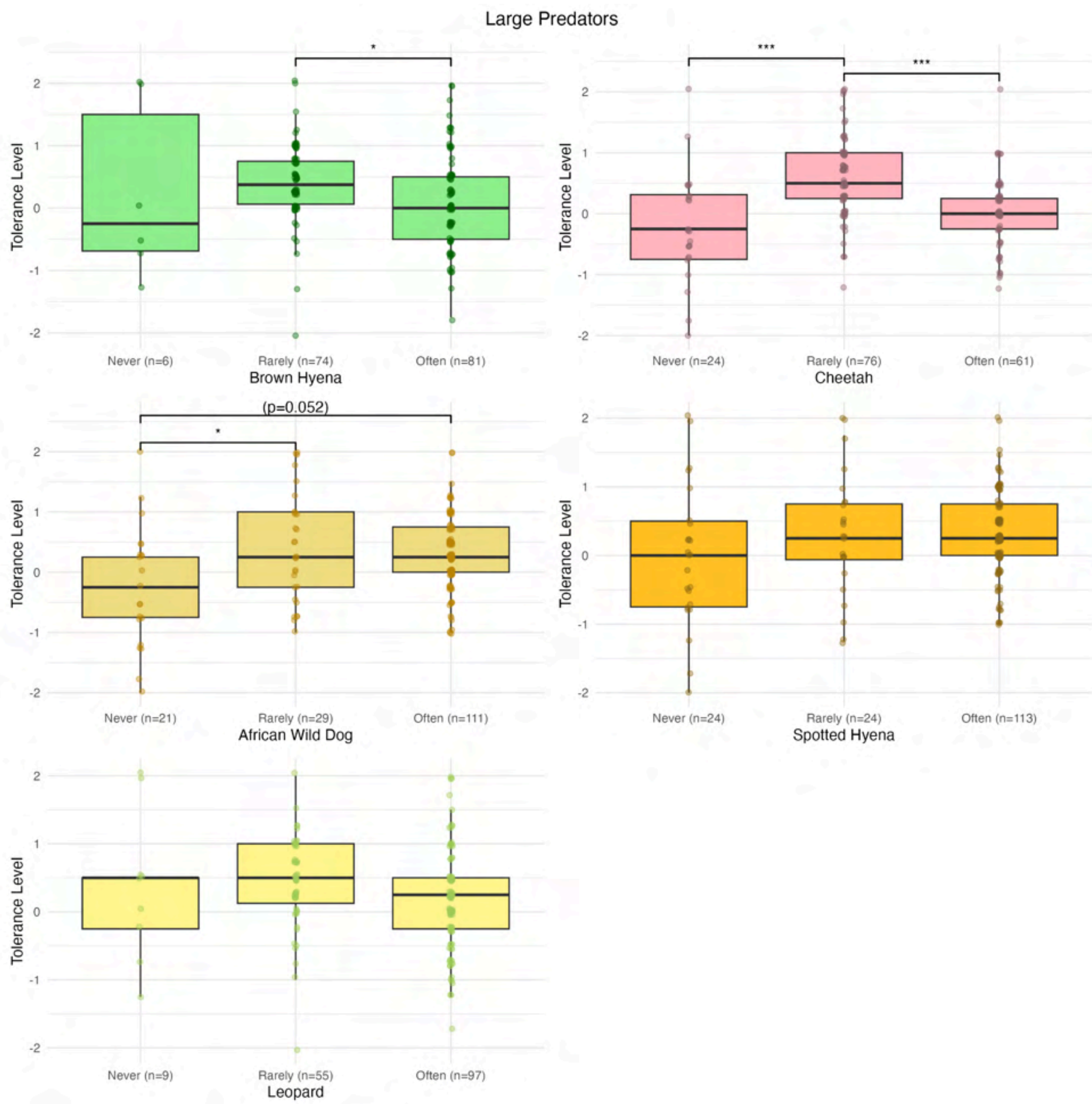


Figure 7A-B. NMDS plot of predator composition per grid cell. Provinces are indicated by color and polygons, LP = Limpopo; NC = Northern Cape; NW = North West. Figure 7A (top) shows overlap in predator compositions between provinces, 7B (bottom) shows relative effect of individual predators on spatial distribution in the plot.

Perceived predator presence and conflict

LMM models for correlations between tolerance and perceived presence show significant results for multiple species individually (Figure 8). There are no large differences in patterns between perceived presence of large predators and mesopredators related to tolerance levels. The intermediate (rarely) perceived presence for African wildcat (p=0.001), brown hyena (p=0.018), caracal (p=0.011) and cheetah (p<0.001) show a significantly higher tolerance level than when they are perceived as often present. Additionally, the cheetah (p<0.001), serval (p=0.006) and African wild dog (p=0.012) also show a significantly higher tolerance for rarely perceived presence in comparison to perceived as never present.
The African wild dog also shows a marginally significant (p=0.052) higher tolerance level when they are often perceived present relative to the never perceived present. For the other predators there are no significant differences in tolerance level between never and often perceived presence. The R^2 values for the models range from 0.04 - 0.16, the lowest R^2 being for the model including the African wild dog and the highest for the model including cheetah. Perceived predator richness does not significantly correlate with tolerance level.



Large Predators
Tolerance Level
Never (n=6)
Rarely (n=74)
Often (n=81)
Brown Hyena
Never (n=24)
Rarely (n=76)
Often (n=61)
Cheetah
(p=0.052)
Never (n=21)
Rarely (n=29)
Often (n=111)
African Wild Dog
Never (n=24)
Rarely (n=24)
Often (n=113)
Spotted Hyena
Never (n=9)
Rarely (n=55)
Often (n=97)
Leopard

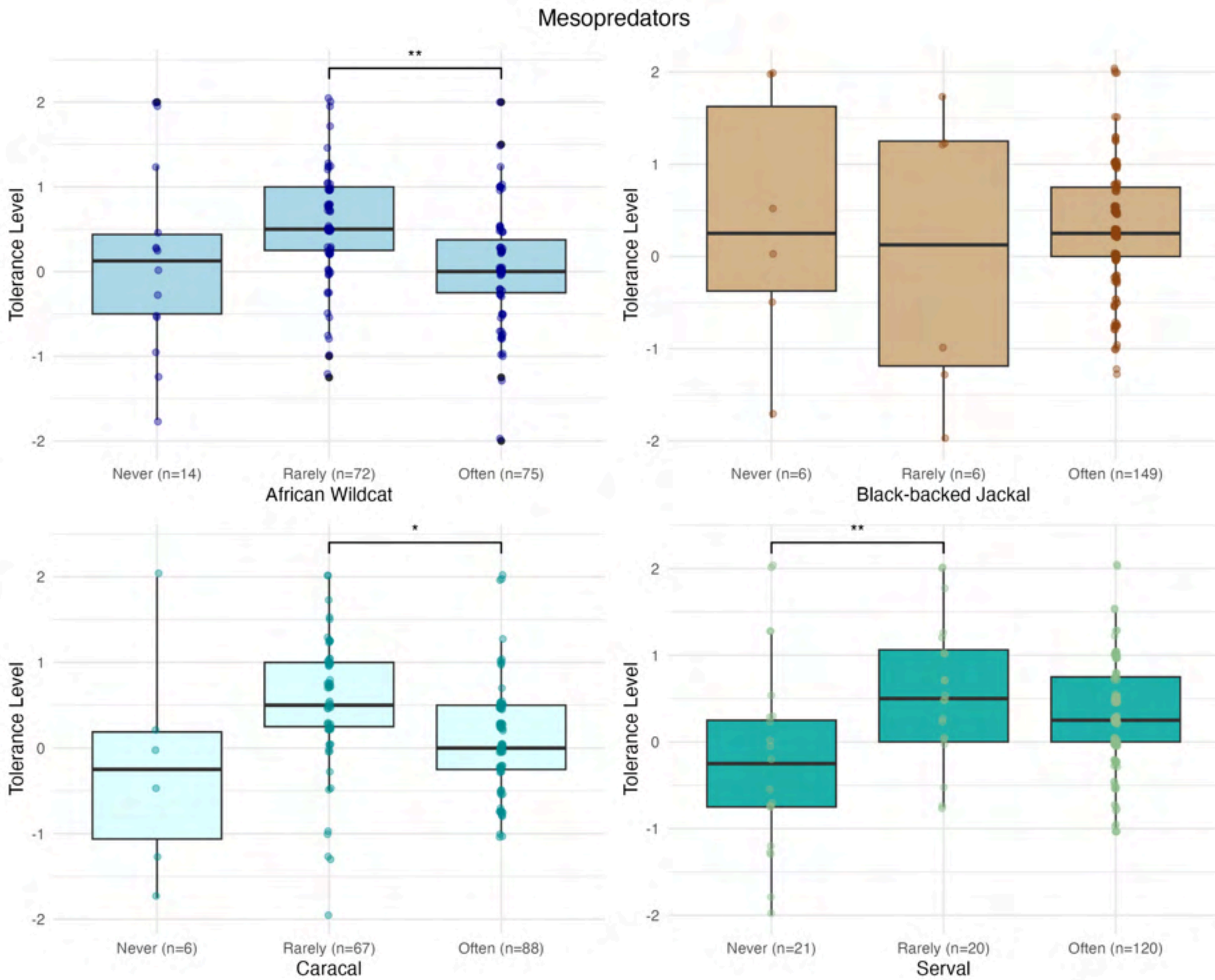


Figure 8A-B. Boxplots for tolerance level per perceived predator presence frequency for large predators (>15kg) (A;top) and mesopredators (<15kg) (B;bottom). Brackets indicate (marginally) significant differences between groups (* = p<0.05; ** = p<0.01; *** = p<0.001).

A total of 130 surveys included responses on the perceived conflict frequency. The models for perceived conflict show a significant increase in tolerance with a decrease in perceived conflict frequency (p<0.001) (Figure 9). A model with the predator richness of species causing perceived conflict shows that with each predator causing conflict the tolerance level decreases with 0.22 (p<0.001) (Figure 10).

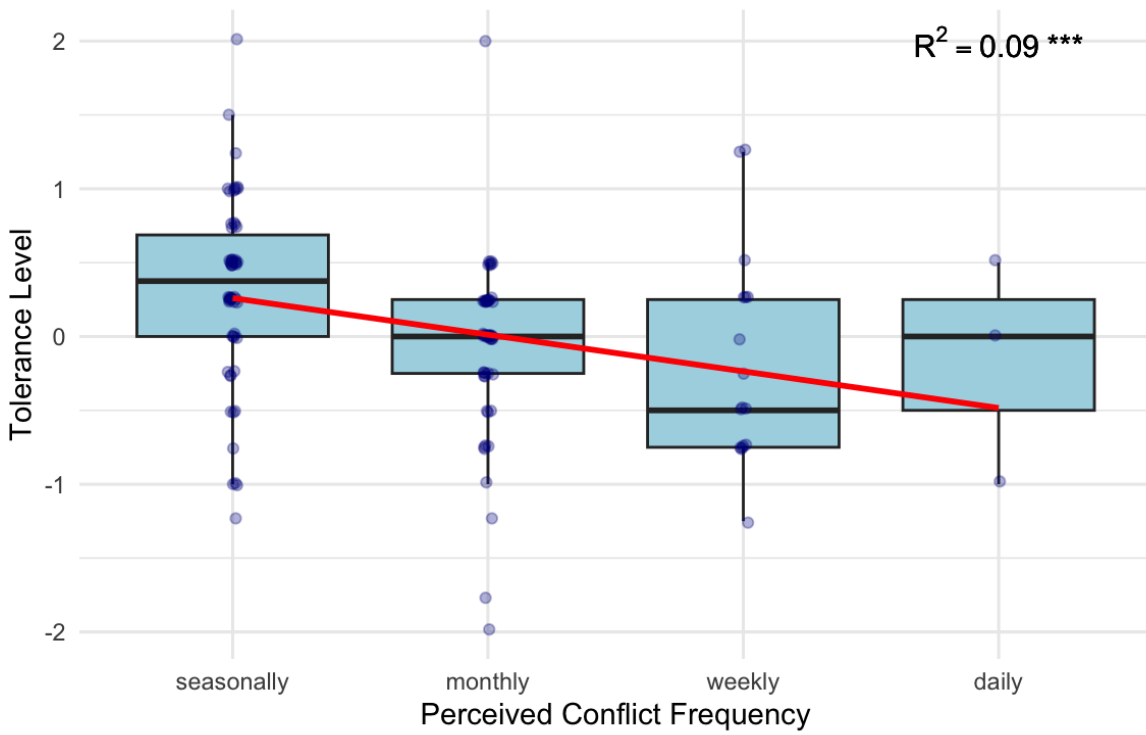


Figure 9. Boxplots of conflict frequency by tolerance level. The red line indicates trend in tolerance level by conflict frequency. (n=130) (*** = $p<0.001$)

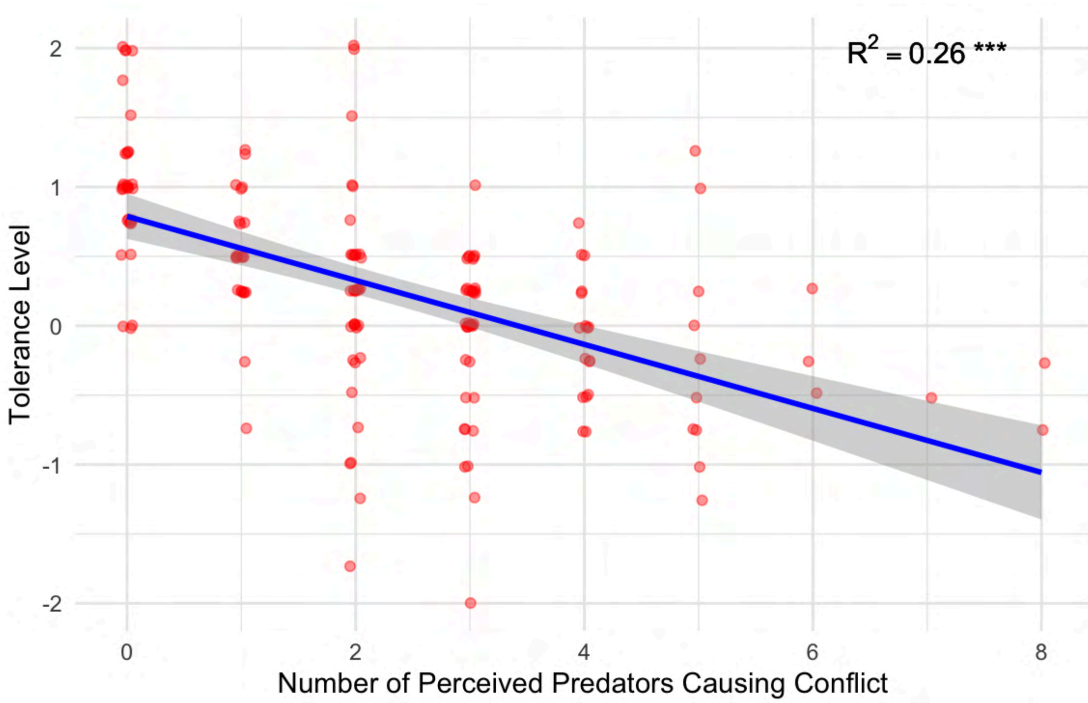


Figure 10. Perceived richness of conflict causing predators by tolerance level. Blue line indicates trend in tolerance level by number of perceived predators causing conflict. Grey area indicates standard error. (n=161) (*** = $p<0.001$)

When testing correlations between perceived predators causing conflict and tolerance level individually all predators but African wild dog, spotted hyena and serval show a significant correlation. Respondents indicating that an individual species is causing conflict significantly correlates with a decrease in tolerance level (Figure 11). The R^2 ranges from 0.09 - 0.23 for all significant models. With the lowest R^2 coming from the brown hyena model and the highest R^2 coming from the black-backed jackal model.

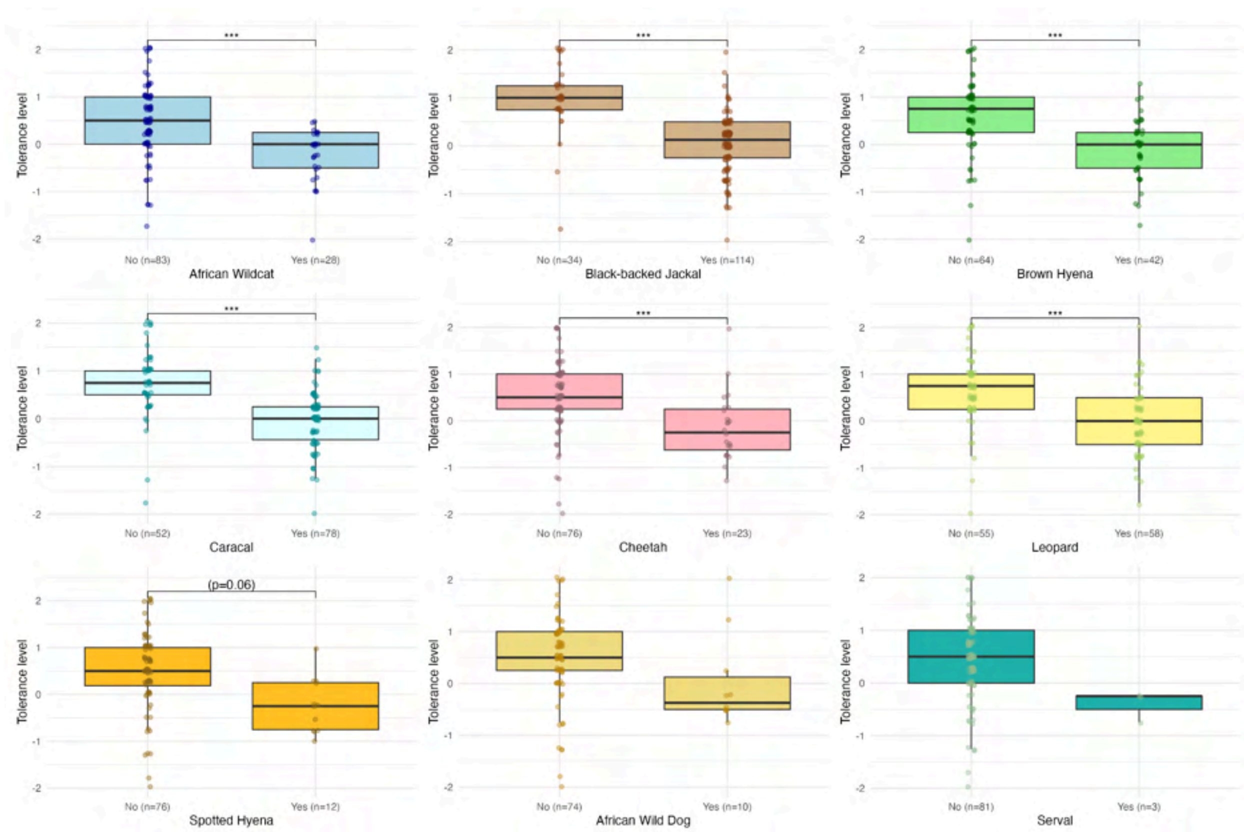


Figure 11. Boxplots for tolerance level per conflict causing species. x=Yes, indicates predators are causing conflict. x=No, indicates predators are not causing conflict. (*** = p<0.001). N is the amount of responses corresponding to that group.

Discussion

The goal of this study was to explore drivers of human tolerance towards predators. Based on the literature it was expected that tolerance towards predators would decline with increasing human-wildlife conflict and higher predator abundances, and to differ between provinces. Furthermore, differences in tolerance were expected between land-use types. To test for correlations between these factors and tolerance, surveys and camera trap observations were used.

This study shows that locally there are correlations between provinces, livestock farms, game farms and perceived conflict with tolerance. Unlike the expectations, only correlations were found between the observed presence of caracals and tolerance and not for any of the other predators. Additionally, there were no links found between the presence of guard dogs and tolerance levels. These results emphasize the necessity to look beyond predator related variables in tolerance studies and tolerance-based conservation.

The tolerance differences between provinces can partially be due to the fact that Limpopo has higher numbers of wildlife tourism than North West and Northern Cape (South African Tourism, 2025). Respondents in Limpopo may experience more direct or indirect positive effects from predators in the form of increased tourism which could result in a higher tolerance towards carnivores (Ohrens et al., 2021). Furthermore, North West has more commercial livestock farming than Limpopo (Maluleke, 2024), so farmers in North West possibly experience more perceived threats for their livestock and economic well being which could lead to a reduction in tolerance.

The tolerance levels varied between grid cells, as indicated by the random effect, suggesting surveys conducted within the same grid cell tended to report more similar tolerance levels than surveys from different grid cells. This non-random variation could reflect social factors, such as local collaborations among respondents or other untested factors like local environmental conditions which may lead to similarities in reported tolerance (Hobson et al., 2024; Seoraj-Pillai & Pillay, 2017).

The lower tolerance for farms with livestock is possibly related to a more direct perceived predation risk on the livestock (Du Plessis et al., 2018), which can result in a decrease in tolerance. Interestingly, the species specific analysis on perceived presence and tolerance level did not show any consistent differences between predators. While some predators have been reported to be causing more damages on livestock farms like black-backed jackal and caracal than others (Niekerk & Nieuwoudt, 2010). These results suggest that perceived predator presence may not accurately reflect either perceived or actual predation risk. Diet analyses of the predators present on livestock farms could therefore distinguish actual livestock predation from perceived threats, and give better insights on predator caused damages. This can be particularly relevant for predators like cheetah, which are being perceived as a threat to livestock, but have been found to avoid preying on livestock even in wild-prey-depleted areas where livestock abundances are high (Forbes et al., 2025). Additionally, the decrease in tolerance with increasing livestock farm size is consistent with findings by Marchini & Macdonald (2012), who reported a positive relationship between farm size and cattle ranchers' intention to kill jaguars.

An increase of tolerance with higher game farm sizes was unexpected, as it was hypothesized that game farms would experience more direct effects of predation or perceived threats by carnivores. A possible explanation for the current results could be that free-roaming predators may be subject to trophy hunting on these larger game farms as it is more likely to have predators present on larger private lands. Giving the game farmers both an economic incentive to tolerate carnivores and a management method to protect their game (Lindsey et al., 2007). Additionally, on game farms it is likely that the animals are less well tagged than on livestock farms. Therefore making it more difficult to distinguish between game casualties or wildlife casualties. Especially on bigger farms it is more likely to have difficulties in distinguishing between game or wildlife. Tolerance of game farmers may therefore be less affected by animal casualties on larger farmers.

The reduction in tolerance with an increase in perceived conflict and relatively high explained variation suggests a possible linear relationship. The low amount of variation explained by perceived conflict suggests that perceived conflict can not be used as an accurate predictor of tolerance, which matches with previous studies (Kansky, 2015; Kansky et al., 2016; Lischka et al., 2019).

The models on perceived presence of predators and tolerance suggest a more complex link to tolerance levels, which is potentially influenced by confounding effects. The higher tolerance for predators that are perceived as rarely present could suggest that the respondents perceive these predators as less of a threat to their well-being or that of their animals. Another possibility is that due to the fact that these predators are reported to be less observed, respondents perceive these species as more valuable due to their (local) rarity (Angulo et al., 2009; Angulo & Courchamp, 2009) and are therefore possibly more tolerant. We should be careful with interpreting predator composition through observations only, as this could be many observations of only one or two individuals. This would probably result in higher tolerance towards a species compared to lower observation numbers, but higher individual count.

The absence of correlations between observed predator presence (excluding caracals) and tolerance level also suggests that there may not be a linear relationship between the two variables for these predators. This could be due to the fact that tolerance is considered to be a behavior that is shaped by people's perception, experiences and beliefs (Brenner & Metcalf, 2020; Hjerm et al., 2020) and therefore not necessarily shaped by actual situations or in this case real predator presence. Additionally, predators being present does not automatically mean that they are also causing conflict with or are threats to the respondents. This means that there also may not be a direct link of predator presence to tolerance through conflict or perceived conflict. The fact that caracal observed presence negatively correlates with tolerance level can however indicate that there is a more direct effect of caracal presence on the livelihoods of the respondents. With the current data it is not possible to quantify the perceived damages that are caused by caracals, but the literature does suggest that caracals significantly impact livestock farms across South-Africa which can explain a decline in tolerance among the respondents when caracals are more abundant (Niekerk & Nieuwoudt, 2010).

The lack of correlation between observed predator presence for most predator species and tolerance backs the findings that tolerance aimed conservation strategies may be more effective in protecting large carnivores that are subject to retaliation due to human-wildlife conflict than predator targeted measures like predator removal (Dolrenry et al., 2020; Frank, 2016; Kansky et al., 2016). Focusing on tolerance in conservation is also a less invasive conservation strategy than some of the currently used practices like for example relocation of carnivores in conflict areas, reducing stress on individuals directly (Dickens et al., 2010). Studies by Zabel and Holm-müller (2008) and Kissui (2008) have shown that raising tolerance by for example financial incentives or education can positively aid in conservation efforts for carnivores.

It is important to consider that the results found in this study are correlational and that the tested factors may not be completely independent. As a consequence, it is important to be cautious with inferring the possible causal relationships between these factors. Additionally, tolerance itself is a complex behavior, which was simplified in this study to allow for statistical analysis and interpretation. A more comprehensive tolerance assessment could benefit the results of this study. Nevertheless, this study is still well executed and gives valuable insights, as

social-science studies are often difficult to interpret and to apply directly as responses can be biased and changing continuously. Furthermore, differences in policies, regulations and enforcement likely also play an important role in shaping tolerance towards predators, however due to difficulties in accessing reliable information on these factors, they were not included in this study.
The results of this study can directly support the application of tolerance targeted conservation strategies locally in the study area and it gives insight into how human tolerance towards predators is shaped on a broader scale. Aiding in the general understanding of human-wildlife conflict and the consequences that may arise from these interactions. Further research should be aimed at exploring more social and economical effects on tolerance level and how this can be effectively applied in conservation strategies.

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Appendix

A. Likert-scale tolerance questions

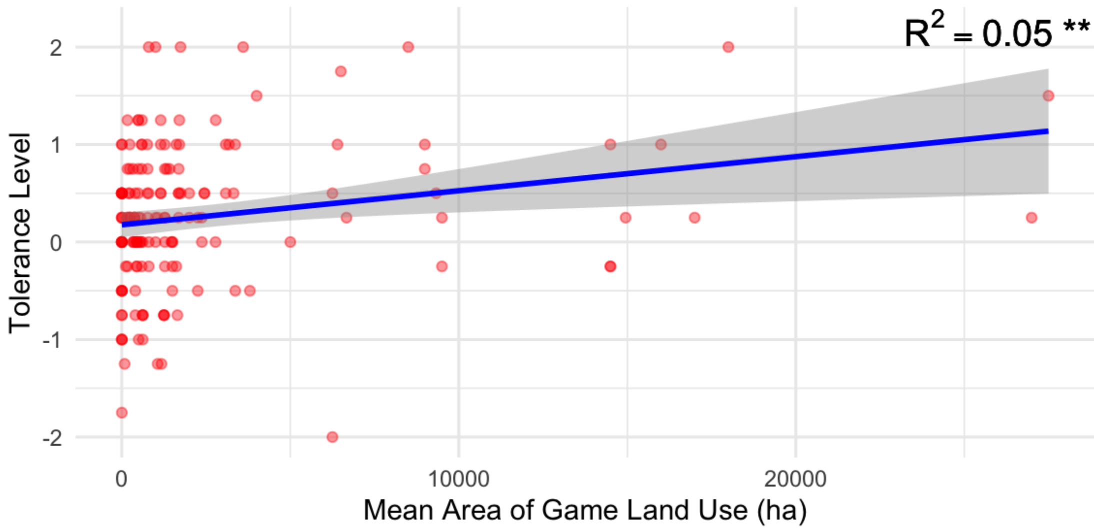
Statement	Strongly disagree	Disagree	Neutral	Agree	Strongly Agree
I am okay with (large) predators on my land	-2	-1	0	1	2
I do not mind predators passing though my land	-2	-1	0	1	2
Small predators do not aggravate me	-2	-1	0	1	2
I do not tolerate large predators	**2**	**1**	**0**	**-1**	**-2**

Table A. Likert scale tolerance questions and answers, including the corresponding scores. The last statement is asked in a reversed style.

B. Camera-trapping protocol

The standardized camera-trapping protocol can be obtained on request from Ashia Cheetah Conservation (marna.smit@ashia.co.za).

C. Land-use size vs tolerance plots



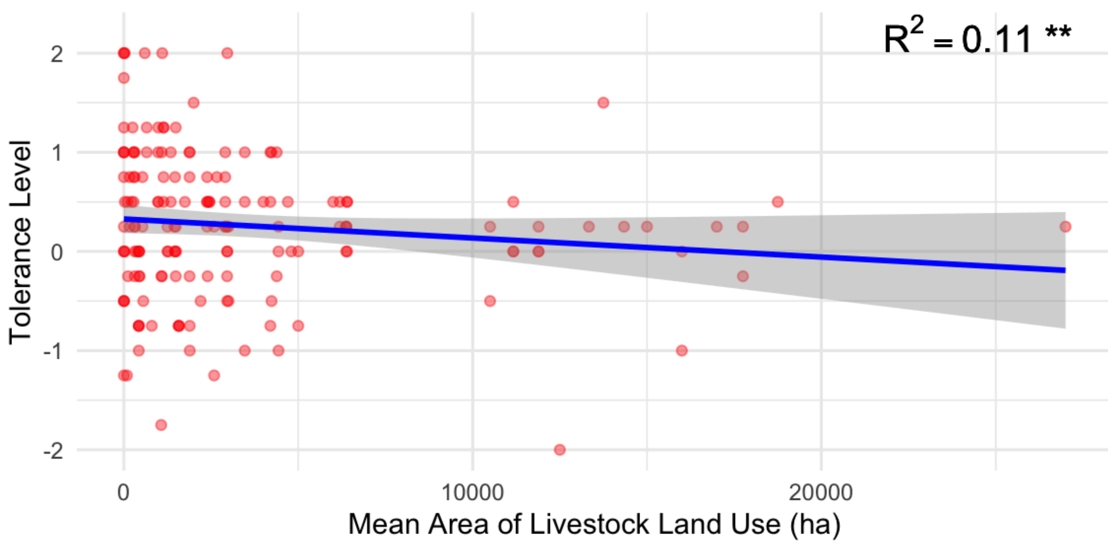


Figure C1-2. Tolerance level by mean area (ha) of land use per grid cell for game (C1;top) and livestock (C2;bottom). Blue line indicates the individual trends in tolerance level with increasing land use size including the standard error. Statistic results for mean livestock area originates from a combined model with mean game area. (**=p<0.01)

D. Observed caracal presence vs tolerance level

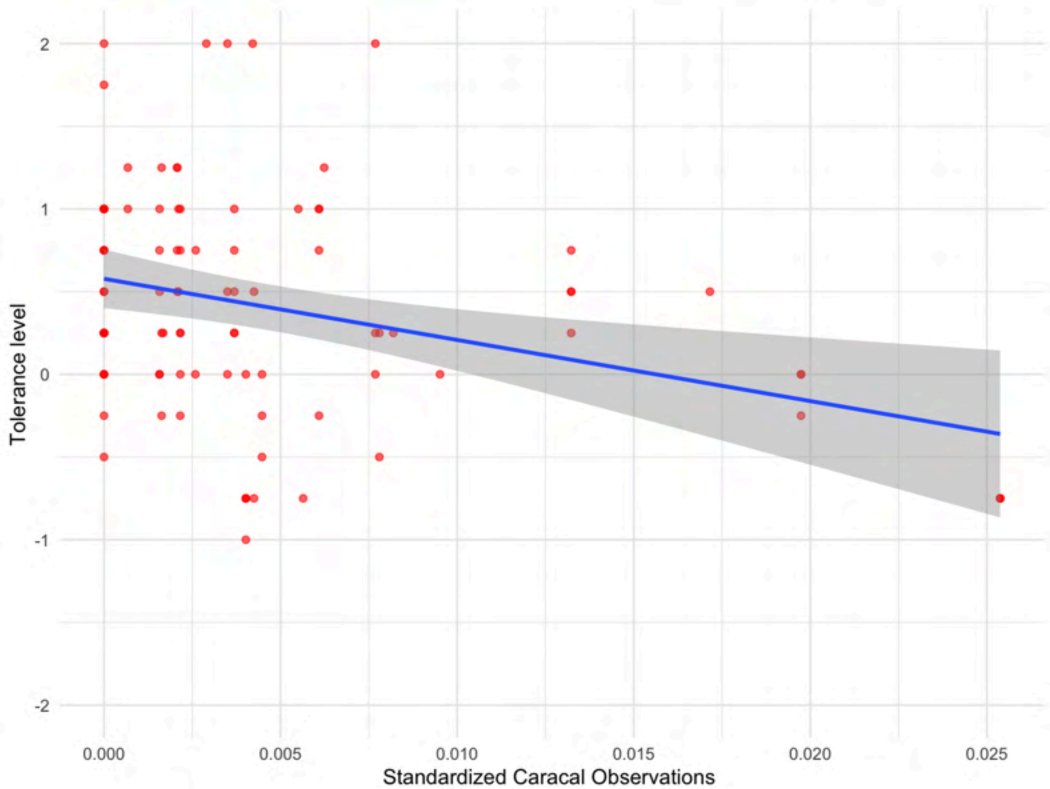


Figure D. Standardized Caracal Observations plotted against tolerance level. Blue line with gray zone indicates correlational trend with standard error.