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Note

Distribution and activity patterns of large carnivores and their implications for human–carnivore conflict management in Namibia

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Abstract: Human–wildlife conflicts (HWCs) are increasing globally and contributing to the decline of wildlife species. In sub-Saharan African countries such as Namibia, most of the suitable land has been or is currently being converted to crop and livestock production to support income or subsistence agriculture. These changes in land use often incur increased levels of HWCs because of crop and livestock depredation by native species. To quantify livestock predation risks posed by carnivores in Namibia, we deployed 30 trail cameras on a 6,500-ha farm in the Khomas region of Namibia from May to July 2018. We developed occupancy models to make inferences about the factors influencing presence and temporal activity patterns of 2 carnivore species. We found that livestock were most at risk from predation by black-backed jackals (*Canis mesomelas*) at night in agricultural areas and from brown hyenas (*Parahyaena brunnea*) at night in riparian habitats. Our results suggest that farmers can reduce HWC risks by implementing animal husbandry practices to include protecting livestock at night using methods such as nighttime corrals and livestock guarding dogs (*C. lupus familiaris*), or herders. Increasing livestock producer access to funding (i.e., individual donations or governmental agencies) to implement improved animal husbandry practices could reduce HWCs.

Key words: agriculture, black-backed jackal, brown hyena, *Canis mesomelas*, carnivores, human–wildlife conflict, livestock, Namibia, *Parahyaena brunnea*, predation

Human–wildlife conflicts (HWCs) are increasing globally and have been implicated as a major factor in wildlife population declines worldwide (Woodroffe and Ginsberg 1998, Gusset et al. 2009). The phrase human–wildlife conflicts encompasses any negative interactions between humans and wildlife—either real or perceived, economic or aesthetic, social or political (Messmer 2000). For humans, HWCs can result in death or injury, relocation, and increased exposure to and risk of zoonotic disease transmission (Carne et al. 2013, Miller et al. 2016, Holland et al. 2018). Additionally, wildlife may be responsible for depredation of livestock, destruction of agricultural crops, and competition with humans for native game species (Holland et al. 2018). In addition to causing significant financial and emotional distress for humans, HWCs can also threaten efforts to conserve wildlife (Madden 2004). For example, humans often kill carnivores that enter agricultural areas (Pangle and Holekamp 2010, Ramesh et al. 2017, Moreira-Arce et al. 2018), and human activities can alter energy expenditure of wildlife by prompting increased vigilance behavior, which reduces available energy for hunting, foraging, mating, and parental care (Benhaiem et al. 2008, Pangle and Holekamp 2010).

In sub-Saharan Africa, increasing demand for arable land continues to degrade biologi-

Figure 1. Spotted hyena (*Crocuta crocuta*), a livestock predator of the Masai Mara National Reserve in Kenya (*photo courtesy of Z. Rossman, taken in Sabi Sands Game Reserve, South Africa, 2017*).

cally rich ecosystems (Ramesh et al. 2017). Large carnivores are particularly susceptible to impacts of agricultural expansion (Pangle and Holekamp 2010, Ramesh et al. 2017), and this expansion continues to increase the prevalence of carnivore–livestock interactions. Large carnivores frequently leave protected areas to hunt in surrounding farmland (Kolowski and Holekamp 2006, Mpakairi et al. 2018). For example, around the Masai Mara National Reserve in Kenya, livestock are routinely depredated by spotted hyenas (*Crocuta crocuta;* Figure 1), lions (*Panthera leo*), and leopards (*P. pardus*; Kolowski and Holekamp 2006). Nearly every continent has shown a history of nationwide lethal predator control in response to similar predation events (Berger 2006).

In Namibia, increasing conversion of wildlands has resulted in large carnivores using agricultural areas, resulting in carnivore population declines and increased human–wildlife conflict (Olbrich et al. 2016). The Namibian economy relies heavily on farming and ecotourism (Snyman 2014); hence, human–wildlife conflict has potential to negatively affect local and national economies. The average annual income of communal farmers in Namibia is approximately $3,260 USD, yet carnivores alone are responsible for an average annual perceived cost of $3,461 USD worth of depredated livestock per person (Rust and Marker 2013). Larger commercial farms do not typically withstand this extreme loss, as they have more resources and thus a greater starting income (Rust and Marker 2013). Although there are compensation programs administered by the Namibian government to help reduce economic hardships on farmers, the programs are underfunded, and farmers are not fully compensated for their losses (Hartman 2017). Because of this burden placed on farmers, they are left with limited options and frequently resort to killing carnivores (Rust and Marker 2013, Humphries et al. 2016, Ramesh et al. 2017). Even if an individual farmer has not accrued any loss from predators, the perceived risk is high enough to trigger their use of lethal control (Berger 2006, Rust and Marker 2013). This type of retaliation has led to declines of carnivores worldwide, including the African wild dog (*Lycaon pictus*; Berger 2006).

Directly measuring livestock depredation risk is difficult because it requires monitoring individual predators and livestock to document predation attempts and mortality events. However, depredation risk can be assessed indirectly using occupancy models (MacKenzie et al. 2017). Occupancy models can be used to draw inferences on spatial variation in carnivore occupancy and temporal variation in carnivore activity, which combined provide information on spatio-temporal variation in predation risk. The key assumption is that predation risk is positively associated with co-occurrence of livestock and carnivores. Results from this type of analysis can provide recommendations for improving livestock management in agricultural landscapes.

Despite extensive research on human–wildlife conflicts, few studies have assessed spatial and temporal variation of livestock predation risk in Namibia. Our primary objective was to understand livestock depredation risk in central Namibia. We designed our study to address the following questions: Where are livestock most vulnerable to depredation, and what time of day is predation risk highest? We predicted that predation risk would vary throughout habitat types and times of day.

Study area

We conducted research on the 6,500-ha Tweespruit farm in the Khomas region of central Namibia from May to July 2018 (Figure 2). The Khomas region is a highland plateau area at an elevation of approximately 1,700 m above sea level. The topography varies greatly throughout the region from mountains and val-

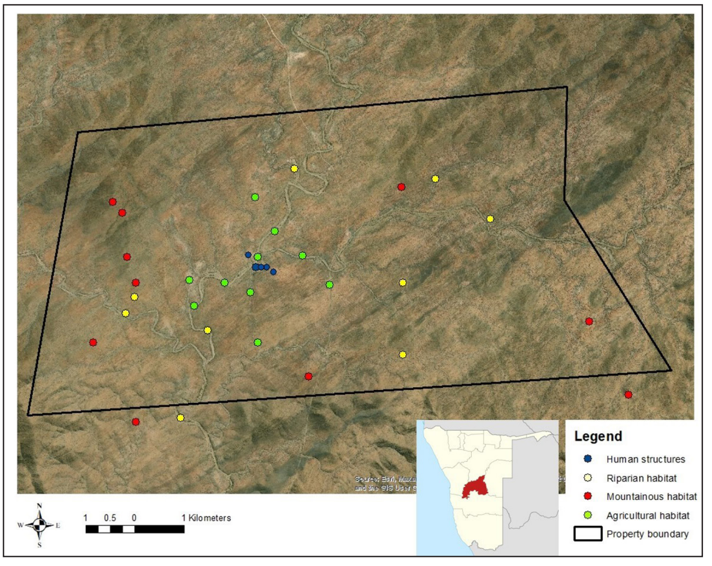

Figure 2. Camera locations among 3 habitat types (agricultural, riparian, mountainous) used in a study of carnivore activity patterns in the Khomas region of Namibia, Africa, May to July 2018.

leys to the flat sands of the Namib Desert. The dry season (winter) lasts from April through November, whereas the wet season (summer) lasts from December through March with an annual rainfall of 370 mm. Tweespruit lies at the confluence of the Nausgomab and Katrus rivers, which has highest flow from February to May and lowest flow from June to January. Little to no vegetation was present on mountain tops. However, in riparian areas, trees often reached heights of 15 m and included species such as *Acacia erioloba* and *Faidherbia albida.* Tweespruit is located on the border of the Namib Desert in a landscape matrix of cattle (*Bos taurus*) and goat (*Capra hircus*) farms. Common fauna consisted of medium-sized herbivores (*Oryx gazelle*, *Tragelaphus strepsiceros*, and *Taurotragus oryx*), primates (*Papio ursinus*), and carnivores (*Canis mesomelas* and *Parahyaena brunnea*). Tweespruit is unfenced except for 2 main livestock camps, a nighttime corral for goats, and a calving area. Livestock guarding dogs (Anatolian Shepherds and mixed breed; 40–65 kg and 20–30 kg, respectively) were present when livestock were in fenced camps. Cattle >10 months old were grazed in unfenced portions of the farm throughout the day and night, unattended by livestock guarding dogs. Cattle <8 months old were kept in a small nighttime corral with their mothers, whereas at 8 months old they are released into a large corral without their mothers to begin the weening process. Goats were released from their nighttime corral into the unfenced portion of the farm at 0700 hours and returned at 1800 hours. During the day, the goat herd was typically accompanied by a livestock guarding dog. These pastoral practices are common throughout the Khomas region.

Methods

We deployed 30 infrared motion-sensored cameras (i.e., trail cameras; Bushnell Trophy Cam Model #119636C, Bushnell Outdoor Products, Overland Park, Kansas, USA) throughout the study area. We used a stratified random sampling design to place 10 cameras each in 3 habitat types: riparian zones, agricultural lands, and mountainous habitat. We used ArcGIS (ArcMap; Environmental Systems Research Institute [ESRI] 2017), satellite imagery (2014 ArcMap basemap; ESRI 2017), and elevation data (Ministry of Economy, Trade, and Industry et al. 2011) to determine habitat type. We delineated riparian habitat by placing a 150-m buffer on either side of the center of the Nausgomab and Katrus rivers. The river buffer was created by taking the widest part of the rivers (100 m), which was measured using satellite imagery in ArcMap, and creating a 100-m buffer on both sides. The 100-m extension past the riverbank incorporated traditional riverside aspects, such as denser vegetation with sandy soils, determined through soil ribbon testing, leading up to the river edge where the substrate becomes a rocky riverbend from the receding river. We delineated agricultural lands by placing a 1.5-km buffer around the human dwelling (center of the agricultural operation). This buffered region was characterized by significant over-browsing by livestock, evident by the lack of understory vegetation and browse line. The agricultural area included farm structures, such as slaughterhouses and night corrals. We classified the mountainous habitat as having an elevation >1,100 m. This cutoff was determined by delineating the toe slopes of the mountain range throughout our entire study area using satellite imagery in ArcMap. We dis-

Table 1. Model description and statistics, such as number of parameter and Akaike's information criterion (AIC) for black-backed jackals (*Canis mesomelas*) and brown hyenas (*Parahyaena brunnea*) in the Khomas region of Namibia, Africa, May to July 2018.

			Black-backed jackal		Brown hyena	
Models	Description	Parameters	AIC	Delta AIC	AIC	Delta AIC
Model 4	Occupancy - function of habitat Detection - function of diel period	7	7524.21	0	409.83	0
Model 2	Detection - function of diel period	5	7536.73	2.52	411.85	2.01
Model 3	Occupancy - function of habitat	4	7671.87	147.65	448.01	38.17
Model 1	Null model	2	7674.34	150.13	450.02	40.18
Model 5	Occupancy - function of distance	3	7676.27	152.06	451.88	42.04

Figure 3. One of 4,248 detections of black-backed jackals (*Canis mesomelas*) in the Khomas region of Namibia, Africa, June 22, 2018. Image was taken in the agricultural habitat.

tributed 10 random points along this line and averaged their elevation values, resulting in the cutoff value of 1,100 m. A 500-m distance restriction between camera locations was placed on the random sampling to ensure independent occurrences.

Cameras were programed to take 1 photo with a 30-second delay. We mounted cameras 20–30 cm above the ground on trees or metal fence posts. We visited cameras weekly to replace batteries, download pictures, and check functionality. The location of each camera and its distance from the human dwelling were recorded using ArcMap distance tool.

We conducted an occupancy analysis in program R (R Core Team 2019) using the package "unmarked" (Fiske and Chandler 2011). We used occupancy (i.e., the probability that a carnivore species occurred at a camera site) as a measure of spatial variation in predation risk, and we used detection probability (i.e., the probability that a carnivore species was detected during a 1-hour period, conditional on the species being present at the site) as a measure of temporal variation in predation risk. Our assessment of predation risk was based on the assumption that depredation risk is highest when predators and livestock are in the same area at the same time (Dulude-de Broin et al. 2020). We divided detection data into hourly periods throughout the 24-hour diel period of our 42-day study. Diel activity patterns of carnivores have been used to assess the landscape of fear concept, which incorporates actual and perceived predation risk (Kohl et al. 2018). We classified each hour as: dawn (0500–0759 hours), day (0800–1659 hours), dusk (1700–1959 hours), and night (2000–0459 hours). We used diel period as a detection covariate. We used combinations of habitat type (agriculture, riparian, mountainous), and distance from human dwelling (m) as occupancy covariates in the models.

We conducted model selection using Akaike's information criterion (AIC; Akaike 1973) and considered the model with the lowest AIC score to be the most supported model (Akaike 1973, Burnham and Anderson 2002). The same models were run for all species that were detected at least 25 times (Table 1). Model 1 was a null model that did not include covariates. Model 2 treated detection probability as a function of diel period, and occupancy probability was constant. Model 3 included habitat-specific occupancy probabilities and constant detection probability. Model 4 included habitat-specific occupancy probabilities and diel period effects on detec-

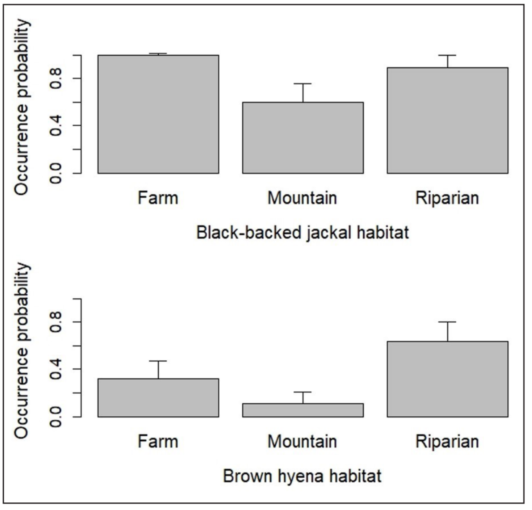

Figure 4. Habitat-specific occupancy probability for black-backed jackals (*Canis mesomelas*) and brown hyenas (*Parahyaena brunnea*) in the Khomas region of Namibia, Africa, May to July 2018.

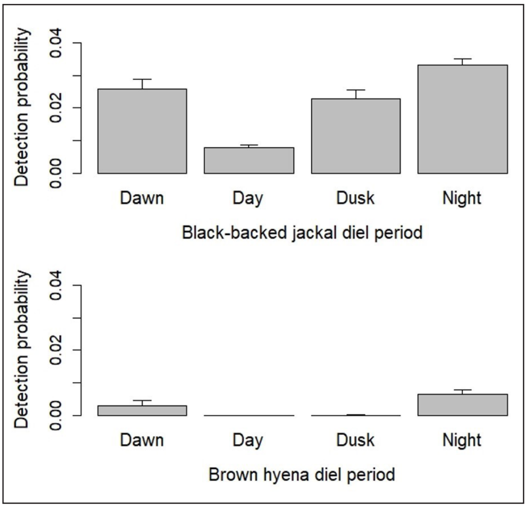

Figure 5. Detection probability for black-backed jackals (*Canis mesomelas*) and brown hyenas (*Parahyaena brunnea*) in the Khomas region of Namibia, Africa, May to July 2018.

tion probability. Model 5 treated occupancy as a function of distance from the human dwelling, and detection probability was constant.

Results

We recorded 4,248 detections of black-backed jackals (*C. mesomelas*; Figure 3), 72 detections of brown hyenas (*P. brunnea*), 5 detections of leopards, and 6 detections of spotted hyenas, for a total of 4,331 detections. We recorded 337.96, 9.92, 1.32, and 0.99 occurrence events per 10,000 sampling occasions (camera hours) for black-backed jackals, brown hyenas, leopards, and spotted hyenas, respectively. There were 5 cameras where no predators were detected. Because of low detection rates of spotted hyenas and leopards, only brown hyenas and jackals were included in the analysis.

The model receiving the most support for black-backed jackals and brown hyenas included habitat type as an occupancy covariate and diel period (time) as a detection covariate. Black-backed jackal occupancy probability was highest in agricultural habitat (0.990 ± 0.009) and lowest in mountainous habitat (0.600 ± 0.154; Figure 4). Black-backed jackal detection probability was highest at night (0.033 ± 0.002) and lowest during the day (0.007 ± 0.001; Figure 5).

Brown hyena occupancy probability was highest in riparian habitat (0.640 ± 0.160) and lowest in mountainous habitat (0.110 ± 0.100; Figure 4). Detection probability was approximately 2 times higher at night (0.006 ± 0.001) than dawn (0.003 ± 0.002; Figure 5). Brown hyenas were rarely detected during the day or at dusk.

Discussion

Our results suggest that black-backed jackals and brown hyenas posed a risk to livestock, as occurrence probability for both species was >0.3 in the agricultural area. Predation risk varied over time for both species, which were primarily active at night and into the dawn hours. These results suggest that mitigating the effects of predation risk by carnivores requires consideration of species-specific activity patterns and habitat use.

Agricultural fields in southern Africa provide abundant prey for carnivores, such as wild game, small mammals, and livestock (Humphries et al. 2016, Ramesh et al. 2017). In addition, it was common for farmers to discard livestock remains from butchering, disease, or predation events, leaving a substantive, easily attainable food supply for scavengers, such as black-backed jackals or brown hyenas to exploit (Kaunda 2001). Similar habitat selection results from jackals in our system were found in Greece with golden jackals (*C. aureus*), which showed preference for agricultural areas as opposed to deeply urbanized areas (Bulmer 2015). Likewise, caracals (*Caracal caracal*), a similar sized carnivore, were found in South African agricultural landscapes to prefer cultivated land and plantations as opposed to more natural grasslands or bushlands (Ramesh et al. 2017).

In agricultural lands of South Africa, brown hyenas had higher densities on livestock farms than comparable game farms (Kent and Hill 2013), attributable to foraging opportunities provided by agricultural operations (Ramesh et al. 2017). Brown hyenas have the physical capability to kill larger livestock species, unlike black-backed jackals, thus increasing the number of potential prey items (Weise et al. 2015). Although brown hyenas have diverse prey species to exploit in agricultural habitats, we noted that brown hyena occurrence was higher in riparian than in agricultural habitat. Higher activity in riparian areas could be due to the availability of water in this habitat, which is a limiting resource in the semi-desert region.

Many African large carnivores are primarily nocturnal. Recent studies found that even species considered diurnal, such as African wild dogs and cheetahs (*Acinonyx jubatus*), have increased nocturnal activity (Cozzi et al. 2012). By using detection probability, we were able to understand activity patterns and thus assess temporal predation risk. We noted that overall, jackals in an agricultural landscape displayed nocturnal and crepuscular behaviors, which aligned with findings for this same species in the Mokolodi Nature Reserve, Botswana (Kaunda 2000). Our results indicate that brown hyena activity was concentrated within a narrower time range than jackals, which were more likely than brown hyenas to be active outside of nighttime hours. Although brown hyena activity patterns are not completely understood, our results supported previous findings for this species (Mills 1978). The temporal activity pattern differences between jackals and brown hyenas were likely due to species-specific behaviors and do not seem to be linked to any anthropomorphic pressure.

Predators were frequently encountered close to human dwellings in our study area. The closest camera was 250 m and had several detections of black-backed jackals. In addition, brown hyenas had the closest detections at 750 m from the human dwellings. These distances demonstrate that, even in the presence of fenced livestock guarding dogs, jackals and brown hyenas are somewhat tolerant of human settlement. Tolerance for human activity and foreign structures has been observed in studies with other jackal species in central Africa and Greece (Vanthomme et al. 2013, Bulmer 2015) and with spotted hyena in Ethiopia (Yirga et al. 2015). The observations we collected of jackals within 250 m of human dwellings occurred at night. In addition, at the 250-m camera, human activity precluded any detections during the time period when most humans were active, as opposed to cameras further from the human dwelling that were more representative of the typical expansive circadian activity patterns of jackal species (Kaunda 2000, Selvan et al. 2019). Additionally, there was a predation event involving a brown hyena on a calf during our study. Because the predator-proof fencing was not maintained, the hyena was able to enter the encampment of the calf and mother through a warthog (*Phacochoerus africanus*) hole. We could not determine the exact time the livestock was predated; however, it occurred within the nighttime hours, which is supported by activity patterns for brown hyenas in our data and previous studies. Taking distance values and predation event into consideration, it was evident that livestock was still at risk even within the enclosures.

Because jackals and hyenas exploit different sized prey, (Weise et al. 2015, Hayward et al. 2017), their effects on livestock, and hence farmers, were likely to differ. In Namibia, 2 typical farming systems arose depending on farmer preference and geographic location of the farm. Famers often maintain several livestock species that differed in size, from small goats (20 kg) to large cattle (580 kg; Rust and Marker 2013, Partner 2018). If the only predators present on the farm were jackals and brown hyenas or solely brown hyenas, our results suggest that livestock were most at risk from 1700 hours until 0759 hours. Thus, farmers should maintain livestock inside predator-proof corrals during this period. Adult bovine cattle were at greatest risk from 2000–0759 hours. However, if jackals were the only predator species, then adult cattle would have little risk of predation, as jackals are approximately 5–15 kg (Kamler et al. 2012, Hayward et al. 2017). We recommended use of predator-proof fencing, livestock guarding dogs, and herders during the times of greatest predation risk, especially with young or injured livestock (Rust and Marker 2013, Nattrass and Conradie 2015).

Mitigation programs have been developed to help resolve human–wildlife conflict issues. Compensation programs managed by governments or non-governmental organizations helped provide financial assistance to individuals who have undergone financial loss through livestock predation. In addition, financial programs aimed at helping farmers build corrals and predator-proof fences could reduce human–wildlife conflict; however, care must be taken so that these efforts do not provide an incentive to expand grazing activities at the expense of wildlife populations. Direct interventions were also used when nuisance animals needed to be relocated (Holland et al. 2018). Most of these programs were geared toward resolving an issue after an event has happened. Data from this study provided farmers with spatial and temporal information on 2 African carnivores to aid in the prevention of livestock predation.

Management implications

Our data provide spatial and temporal information about local predator visitation to a farm; this information should be used to guide preventative management. We recommend preventing livestock from entering high-risk areas during risky times. Corralling livestock from 1700 hours until 0759 hours would reduce exposure to predation. In addition, it is important to reiterate that maintaining the integrity of the predator-proof fencing is crucial in protecting livestock as displayed by the predation event during our study. Although the carnivores in our system were most active at night, it would be beneficial to deter livestock from entering riparian areas during the day to further reduce the opportunities for encounters with brown hyenas.

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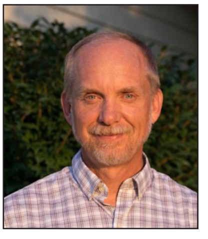

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