



Teeth, tusks, and spikes: Repeated den sharing between predator and prey in an African Savannah

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Abstract

We have been monitoring spotted hyaena dens with camera traps at our site since 2016. We describe a novel phenomenon: concurrent subterranean den sharing between spotted hyaenas, warthogs, and crested porcupines at a wildlife conservancy in Kenya. We discovered two different hyaena clans that occasionally shared active dens with warthogs and porcupines in 2016, 2017, 2018, and 2019 but not since. We speculate on the reasons why and how this cohabitation arrangement arose and suggest that it might be based on a 'healthy respect' for the threats presented by their mutually formidable weaponry. We hope this note will encourage others to describe similar behaviour.

Résumé

Depuis 2016, nous surveillons les tanières de hyènes tachetées à l'aide de pièges photographiques sur notre site. Nous décrivons un phénomène nouveau: le partage simultané de tanières souterraines entre hyènes tachetées, phacochères et porcs-épics à crête dans une réserve naturelle du Kenya. Nous avons découvert deux clans de hyènes différents qui partageaient occasionnellement des tanières actives avec des phacochères et des porcs-épics en 2016, 2017, 2018 et 2019, mais pas avant. Nous nous interrogeons sur les raisons et les modalités de cette cohabitation et suggérons qu'elle pourrait être fondée sur un "respect sain" des menaces présentées par leurs armes mutuellement redoutables. Nous espérons que cette note encouragera d'autres personnes à décrire un comportement similaire.

The majority of mammals are known to use dens (Kinlaw, 1999). Dens are burrows or lairs that function as places to raise offspring, rest sites, and shelters (Oli et al., 1997). Dens may be above or below ground, and their substrate is usually earth, stone, or wood (Roper et al., 2001). The same den may be used by multiple mammalian species at once, even those that ostensibly should not peacefully coexist, such as intraguild competitors, or predators and prey (Mori et al., 2015).

Den sharing has been noted before as far back as the Early Triassic between a carnivorous proto-mammal cynodont *Thrinaxodon*

liorhinus, and its potential prey – a temnospondyl amphibian *Broomistega putterilli* (Fernandez et al., 2013). Previous research has found that extant predators with similar niches may also peacefully share dens (Macdonald et al., 2004). Sometimes, predators and prey can also exhibit such behaviour: one study found that red foxes (*Vulpes vulpes*) shared dens with multiple rodent species in Japan (Kondo, 2018). Other studies described the cohabitation of crested porcupines (*Hystrix cristata*), red foxes, and European badgers in Italy (*Meles meles*; Coppola et al., 2022; Mori & Menchetti, 2019). Thus,

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den sharing is known to occur across multiple taxa and in various ecosystems, though whether it occurs in tropical ecosystems, such as those in sub-Saharan Africa, remains largely unknown.

Spotted hyaenas (*Crocuta crocuta*; hereafter 'hyaenas') are the most abundant member of the large carnivore guild in sub-Saharan Africa (Watts & Holekamp, 2009). Female hyaenas give birth at natal dens prior to transferring their cubs to the clan's communal den 1–2 weeks later (Holekamp & Smale, 1998). A clan may cycle between multiple dens within its territory over the course of a year; the same den may be used sporadically for decades (Lansing et al., 2009). Common warthogs (*Phacochoerus africanus*; hereafter 'warthogs') which share much of their range with that of hyaenas, make use of dens as nocturnal refuges from predators (Somers et al., 1995). Multiple females may use the same den for cooperative defence (White & Cameron, 2009), and piglets will enter the den prior to their mother when fleeing predators. Finally, across much of the region, crested porcupines (*Hystrix cristata*; hereafter 'porcupines') also make use of dens to give birth to young and as daytime shelters (Monetti et al., 2005; Viviano et al., 2020).

Past research has documented the occupation of hyaena dens by other species, including warthogs and porcupines (Boydston et al., 2006; authors' observation) but did not publish observations of concurrent usage. We are aware of only one event of potential concurrent den usage (using different entrances) between hyaena and warthog that was documented during a seasonal flood in the

Okavango Delta, Botswana (Joubert et al., 2019). Hyaenas are apex predators capable of hunting prey many times their own size (Holekamp et al., 1997). Furthermore, at our study site and in other areas across their range, hyaenas are known to prey both on warthogs and porcupines (Davidson et al., 2019; Hayward, 2006). Thus, warthogs and porcupines place themselves at risk if they share dens with hyaenas.

It is important to note, however, that both warthogs and porcupines are well-armed against predation. Warthogs have sharp tusks and a compact, powerful build. Porcupines have long, rigid quills (up to 30 cm), which makes them formidable prey (Mori et al., 2014). Dangerous as these armours already are, the threat they present is amplified to a predator encountering them in the close quarters of a subterranean den.

We describe and interpret concurrent den sharing between hyaenas, warthogs, and porcupines at a wildlife conservancy in Kenya.

1 | METHODS

This study was carried out between Jan 2016 and Dec 2021 at the Lewa Wildlife Conservancy (LWC), and Borana Conservancy (BC) in Kenya, straddling the border of Meru and Laikipia counties (0.20° North, 37.42° East). The total area of this site is 375 km² (LWC=250 km²; BC=125 km²). During the study period, we

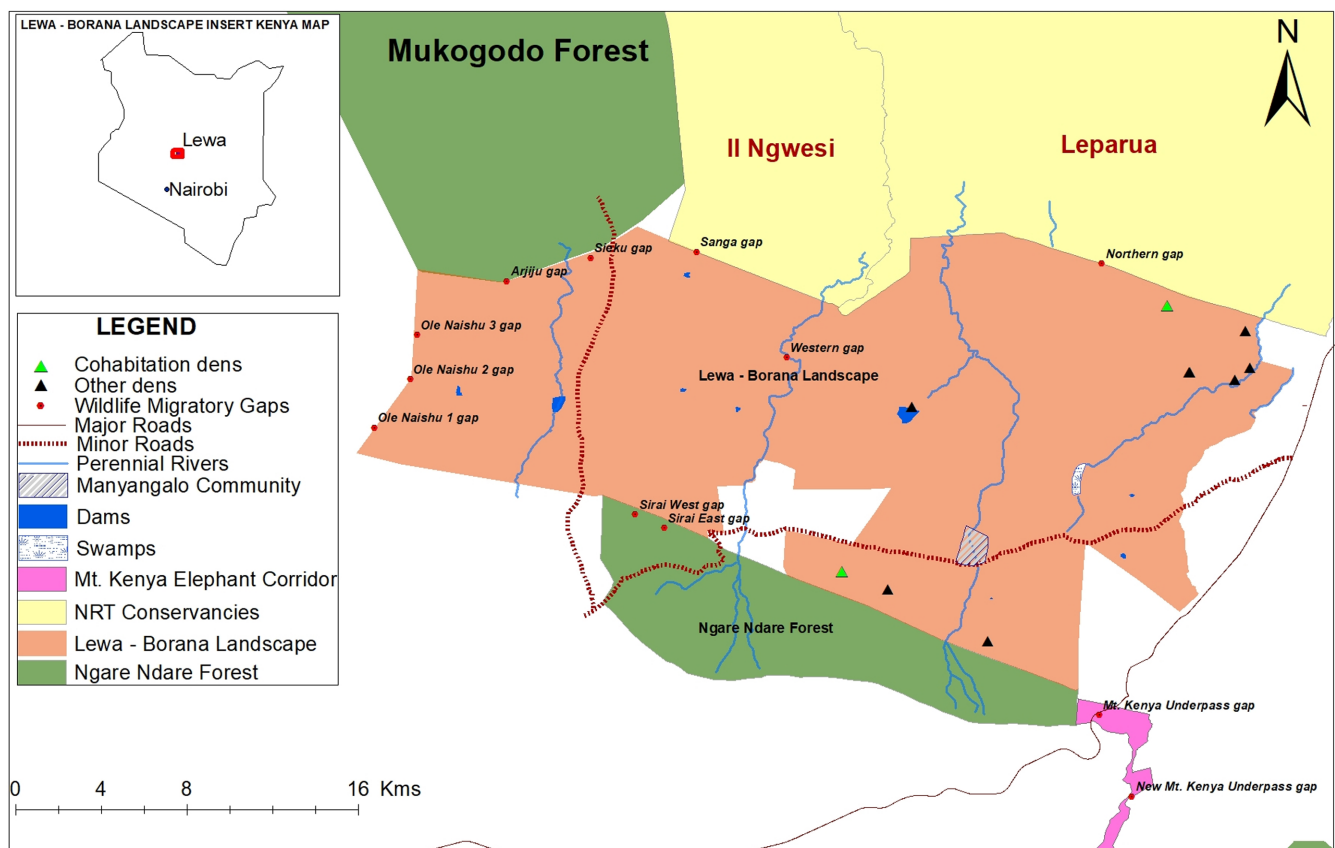


FIGURE 1 Map of Lewa-Borana landscape with hyaena den locations (indicating which dens had cohabitation).

monitored five communal hyaena clans at five separate dens and set up camera traps [Reconyx (Holmen, WI, USA) and Bushnell (Kansas City, KS, USA)] at the entrances to each of these dens (Figure 1). Camera traps were checked weekly or bi-weekly. We counted concurrent usage of a den when we found photographic evidence of either a warthog or a porcupine entering and exiting an active hyaena den. We defined hyaena dens as active by photographing individual hyaenas entering and exiting the dens before and after the detection of warthog or porcupine. We determined the individual hyaena clans by a combination of physical features of matriarch (examining photographs), tracking (we had VHF collars on members of different clans), geographical separation, and individual clan composition (for more details on methods, see Dheer, 2016).

2 | RESULTS

Out of the five active hyaena dens we monitored, we detected concurrent den usage at two separate dens of two separate hyaena clans. Two dens had a tri-species den usage, while the other three monitored hyaena dens were only occupied by hyaenas.

In den #1, camera trap data revealed that there were two porcupines, three warthogs, and seven hyaenas occupying the den between January–March 2016 and January–March 2017. In den #2, we found two porcupines, six warthogs, and 11 hyaenas living in the same den between March–April 2018 and between March–May 2019. These cohabitations lasted a total of 24 weeks at den #1 and 20 weeks at den #2 with daily departures and re-entries using the same den entrance over those time periods and sometimes at remarkably close intervals (less than 5 minutes).

3 | DISCUSSION

How do we make sense of this cohabitation? For one, temporal partitioning may play a role: hyaenas and porcupines are mostly nocturnal, and warthogs are mostly diurnal (Estes, 2012) so shared dens could be occupied on a ‘time-share’ basis (or, with some temporal separation). Yet, we found evidence of all three species being inside at the same time. Although we have not dug the dens to verify for multiple chambers, we assume that these dens have a subterranean layout with branches and chambers that are occupied by the different species. Using specialised camera equipment may shed light on how the species are spatially separated.

Furthermore, our study site is composed of hard volcanic murram soil (pisolitic iron oxide laterite) over Archean basement rocks (Linsen & Giesen, 1983), which may make digging new dens a challenge. We observed cohabitation occurring during the dry season when the hardened ground might have made digging new dens more difficult. Cohabitation seemed to end with the start of the rains (in April and May), which would have softened the soil. Thus, another plausible explanation is that the type of soil at LWC and BC makes digging new dens an energetically inefficient endeavour. However,

even with a prolonged drought in 2020, 2021, and 2022, we have not seen any new instances of cohabitation, leaving us to search for other explanations.

At these specific hyaena dens, we discovered bones of large prey such as African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), and regurgitated pellets containing the skin and hairs of livestock, but no signs of warthog or porcupine. Porcupines may seek out and consume the bones accumulated inside hyaena dens (Mori et al., 2018). Other potential factors that might help explain cohabitation tolerance are prey selection and acquisition behaviours. Although we detected both warthog and porcupine in the scat of other hyaenas at our study site (Davidson et al., 2019), we did not detect any hairs of these prey species in the scat of the two cohabitating clans, raising questions about clan prey selectivity. We suspect different hyaena clans may display particular tendencies in regard to their foraging habits and prey selection. However, the cohabiting clans had never been observed hunting or scavenging, so this distinction cannot yet be made. More research on the diets and foraging behaviour of different hyaena clans resident in LWC and BC will be useful to understand how this cohabitation occurs.

AUTHOR CONTRIBUTIONS

Study design: Marc Dupuis-Désormeaux, Zeke Davidson, Suzanne E. MacDonald; fieldwork: Arjun Dheer, Saibala Gilisho, Timothy N. Kaaria; data analysis, writing: Marc Dupuis-Désormeaux, Arjun Dheer, Saibala Gilisho, Timothy N. Kaaria, Zeke Davidson, Suzanne E. MacDonald.

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CONFLICT OF INTEREST STATEMENT

None.

DAT A AVAILABILITY STATEMENT

Photographic data are stored at LWC can be obtained by writing to timothy.kaaria@lewa.org

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