**The dark side of the moon – A crepuscular cursorial hunting species reduces its daytime activity ….**

**…. prior to moonlit nights**

**… dependent on prospective moonlight intensity**

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ABSTRACT

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INTRODUCTION

Moonlit nights have often been related to mystical and esoteric events in the human and animal world. Folklore aside, it is no doubt that moonlight influences many ecological processes such as, for example, overall diel activity patterns (Lang et al. 2006, Cozzi et al. 2012), predator-prey relationships (Lima and Dill 1990, Prugh et al. 2014), movement behaviours (Polansky et al. 2010, Kamrowski et al. 2015, Last et al. 2016), and feeding habits (Elangovan and Marimuth 2001, Riou and Hamer 2008, Rubolini et al. 2015, Preston et al. 2019) across many taxa (reviewed in Kronfeld-Schor et al. 2013).

While daytime lighting and temperature conditions are fairly stable across consecutive weeks (substantial changes occur at monthly or seasonal scales), night-time light conditions change daily (Kronfeld-Schor et al. 2013). Within two weeks only, night illuminance varies from 0.3 lux under bright full moon conditions to < 0.002 lux on a dark moonless night (Kyba et al. 2017). Additional variability in the night-time light availability and intensity is caused by differences in the timing of moon rise and moon set within the 29.5 days lunar month cycle. While during the waning phase the moon is in the sky during the first part of the night, during the waxing phase it only rises later at night. This variability raises the questions of how different species budget for their diel activities, whether they adjust their daytime activity dependent on prospective moonlight availability and intensity, and which strategies and cues they develop to maximize activity during the most favourable hours of the 24-h cycle.

The effect of environmental light and temperature on animal activity is dampened or reinforced by the biotic environment, and by ecological and physiological constraints. For instance, the consequences of moonlight on foraging and predation are well documented and rest on the assumption that when the risk of predation outweighs the increase in foraging success, a lower level of activity during moonlit nights is expected, and vice versa (Lima and Dill 1990, Kronfeld-Schor et al. 2013). In Queen Elizabeth National Park in Uganda and in Tanzania’s Ngorongoro Crater, lion (*Panthera leo*) hunting success was highest during dark nights (Vanorsdol 1984, Packer et al. 2011), probably due to the species ambush hunting technique and the advantage conferred by darkness over its prey. Inversely, many rodent species that suffer predation by species whose efficiency increases during full moon nights reduce their activity on moonlit nights (Kotler et al. 1991, Gutman and Dayan, 2005). Furthermore, part of the influence of moonlight on several life history traits is arguably linked to animal physiological constraints (e.g., visual acuity) and to the contrast between lighting and temperature conditions at night and during the day. This dyadic effect is particularly relevant for species that are limited in their activities by high temperatures (and would therefore benefit from shifting their activity to the cooler night-time hours) but that require sufficient lighting conditions (therefore benefitting from shifting their activity to daytime hours). The crepuscular habits of cursorial hunting species such as wolves (*Canis lupus*), African wild dogs (*Lycaon pictus*), and cheetahs (*Acinonyx jubatus*) are undoubtedly partly controlled by such trade-off (Theuerkauf et al. 2003, Cozzi et al. 2012, Broekhuis et al. 2014).

The African wild dog (AWD) lives in packs averaging 8-12 adults and their dependent offspring (REF). AWDs are mainly active and hunt twice a day, primarily during early mornings and later in the evenings, but hunting also occurs during moonlit nights (Estes and Goddard 1967, Cozzi et al. 2012). AWDs are cursorial hunters and chase their prey on sight for up to few kilometres (Creel and Creel 2002). This hunting technique requires good visibility and cooler temperatures. AWDs are characterised by a high energetic requirements and metabolism;, and within 6 to 8 hours after a full meal the pack is typically ready to hunt again. As such, hunting activities are only little influenced by the hunting effort and success of the previous hunting burst. AWDs have been proposed to adjust activities and life history traits to facilitate thermoregulation in hot climates and periods (McNutt et al. 2019). The species’ night-time activity patterns are not top-down regulated by the night-time activity of stronger competitors such as lions and spotted hyenas (*Crocuta Crocuta*) (Cozzi et al. 2012). It can thus be anticipated that, to take full advantage of the multiplicative effect of best lighting and temperature conditions, AWDs trade daytime activity for activity during the night. ~~The question remains as to whether AWDs adjust their evening activity in anticipation of the prospective moonlight conditions.~~

We used activity data collected between 2007 and 2021 on XXX free-living AWD by means of radio collars fitted with accelerometers to investigate (i) under which lighting conditions is night-time activity comparable to daytime activity, (ii) whether evening activity is reduced in anticipation of bright moonlit nights, and (iii) conditions under waxing and waning regimes elicit different activity patterns.

MATERIAL AND METHODS

*Study area*

This study was conducted between 2007 and 2021 on a free-living population of African wild dogs in the Okavango Delta ecosystem in Northern Botswana. The area is characterised by a wet season between November and March/April and a dry season between April/May and October during which time cloud cover is virtually non-existent. October and November are typically the hottest months of the year and June and July the coolest (Mendelson 2010). The area is a mosaic of habitat types including floodplains, mixed woodlands acacia (*Acacia spp.*) dominated, and mopane forests (Mendelson 2010; Cozzi et al. 2013a). All major prey species as well as other large carnivores are present in the area, and human activities are restricted to tourism-related activities. (Cozzi et al. 2012, Cozzi et al. 2013a, 2013b).

*Data collection*

We used radio-collars equipped with accelerometer sensors (Vectronics Aerospace GmbH, Germany) to obtain continuous activity data. A Botswana-registered wildlife veterinarian was responsible for all immobilization procedures for the purpose of fitting radio-collars, as specified under Research Permits EWT 8/36/4 XXXVIII(15) and EWT 8/36/4 XXXVI (33) and issued by the Botswana Ministry of Environment, which regulates animal care and use. Following Osofsky et al. (1996), we anesthetized adult AWDs using a combination of ketamine, xylazine, and atropine, and reversed with yohimbine. After immobilization, the collared individuals safely rejoined their pack showing no signs of distress.

The collar sensors record acceleration at 4 Hz along the X and Y axes and sum them over 5 minutes intervals; a raw activity data point thus consists of the number of acceleration counts per 5 minutes (Cozzi et al. 2012). Following Cozzi et al. (2012), we used a threshold of 15 (or 20?) counts per 5 minutes to identify resting, inactive animals. The truthfulness of this threshold was corroborated by the fact that between 12:00 and 16:00 (later referred to as inactive period), time during which, irrespective of the season, AWDs almost always rest (G Cozzi, pers. obs.), mean activity values were XXX counts (Appendix A1). We collected data from XXX packs for a mean of XXX days/pack (range, XXX–yyy d). Owing to the collective movement of pack members, when more than one individual was collared in a single pack, we only considered data from a single individual.

Environmental variables were readily available online. We obtained temperature data from XXXX. XXX returns temperature values at 2 m above ground on a Y km2 grid (Ref). We acquired rain and cloud cover data at hh-hours intervals on a NN km2 grid from FFF (Ref). We obtained information on moonrise, moonset, percentage moon illuminated, angle and altitude from the horizon from GGG (Ref).

*Data analysis*

Since AWDs don’t necessarily rest during the night (Cozzi et al. 2012), we considered as “AWD day” the 24 h period starting at 14:00, the time of lowest activity (Appendix A1). To infer the exact daily transition time between the inactive and the active period (i.e., the period between 16:00 and 12:00 on the consecutive day), we applied a threshold of a minimum of 30 minutes of consecutive activity data with values > 15 counts. The rational for this threshold is explained in Appendix A1. Here and elsewhere, we only considered activity data along the X (surge) axis, for values along this axis are not influenced by the position of the collar that may twist around the animal’s neck (Chakravarty et al. 2019).

RESULTS

DISCUSSION

Appendix A1

Chart

Description automatically generated**Figure S1** (TO BE REDONE WITH NEW DATA)**: Average activity values across all collared individuals used in this study**. The period between 12:00 and 16:00 is referred to as inactive period. During this period, AWDs almost always rest, irrespective of the season. We considered a “AWD day” the 24 hours period starting at 14:00, the time of lowest activity within the inactive period. The horizontal line shows the 15 counts threshold.

Within the inactive period, single data points well-above the threshold of 15 (?) 20 (?) counts/5 min were observed. Such values are likely related to activities such as grooming, playing, drinking, rolling, or other “stationary” behaviours, namely behaviours that do not involve a noticeable spatial displacement. We used activity data during the inactive period to obtain a threshold to discriminate between “stationary” activities such as the one just described and extended period of “real” activity during which the pack moves and hunts across its territory. Such a threshold is crucial to infer the exact daily transition time between the inactive and the active period (i.e., the period between 16:00 and 12:00 on the consecutive day). For this, we investigated the distribution of consecutive activity data points with values > 15 (?) 20 (?) acceleration counts during the inactivity period (Figure S2). In 5 % of the cases, we observed 6 or more consecutive data points with values > 15 counts. Because, even in the inactive phase, it can’t be excluded that a few (we regarded 5 % of the cases as realistic) “real” activity events will happen, we deemed the threshold of 30 min (corresponding to six or more consecutive data points with values > 15 counts) as appropriate. This threshold holds also from a biological point of view of the species, as inferred by our (G Cozzi, JW McNutt) long-term observations in the field: During the inactive phase, playful activities do occur, but adult individuals rarely take part in these activities for long periods of time exceeding 10 minutes. “Real” activity events sensu this manuscript are very rare but can happen during the inactive phase, such as an exceptional late (respectively early) return to (departure from) the den during the denning season. During the active period, short stationary activity events that may not be considered “real” activity sensu this manuscript can be greeting ceremonies. Usually, pack members greet each other prior hunting rellies (Walker et al. 2017). In some cases, however, after the greetings, pack members go back to rest at the same place or move a few hundred meters before resting, instead of going off hunting. In such cases, greetings and the associated movements are unlikely to last more than 15-20 minutes.

Based on the above considerations, we used this 30 min threshold to infer the exact daily transition time between the inactive and the active period, i.e., the beginning of the daily activity that follows resting during the hot hours after noon.

1 2. 3. 4. 5. 6 or more

95%

Figure S2