PHOTOGRAPHIC AND IDENTIFICATION PROTOCOL

Using camera traps to study hyenas: challenges, opportunities, and outlook

Arjun Dheer[1] · Dinal Samarasinghe[2] · Stephanie M. Dloniak[3] · Alexander Braczkowski[4]

Abstract

The use of remote camera traps has accelerated rapidly in the field of large carnivore science since the 1990s. Members of the *Hyaenidae* are important components of functional ecosystems in Africa and parts of the Middle East and South Asia, and make good candidates for study using camera traps. However, camera trap studies of hyenas remain rare in the literature when compared to species like tigers *Panthera tigris*, leopards *Panthera pardus*, and snow leopards *Panthera uncia*. In this paper, we examine the published use of camera traps for hyenas ($n = 34$ studies implemented between 2007 and 2020) and examine the logistical challenges of using camera traps, such as individual identification, limited sexual dimorphism, and complex social structures, for studies of hyena population biology, behavioral ecology, and conservation. We highlight what these challenges may mean for data analyses and interpretation. We also suggest potential benefits of further camera trap studies of this taxonomic family, including new insights into social behavior, range extensions, and robust density estimates.

Introduction

Since Karanth's (1995) seminal paper using camera traps to estimate tiger densities with spatially explicit capture–recapture (SECR) models (White et al. 1982), the application of camera traps in wildlife research has expanded rapidly.

✉ Arjun Dheer
arjdheer@gmail.com

1 Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, 10315 Berlin, Germany

2 Wildlife Research and Nature Conservation Foundation (WRNCF), 487/4 Old Road, Kottawa,, Pannipitiya 10230, Sri Lanka

3 Department of Integrative Biology, Michigan State University, East Lansing, MI 45524, USA

4 School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzen, China

Camera traps have since been used to answer a myriad of ecological and applied conservation questions including density estimation, spatiotemporal activity patterns, and occupancy, and on organisms ranging from insects (Suckling et al. 2020) to African elephants *Loxodonta africana* (Moolman et al. 2019). As such, camera traps have transformed scientific understanding of mammalian distributions and assemblages (Rowcliffe and Carbone 2008). In particular, camera traps have found utility by scientists studying large carnivores, as these animals typically have large home ranges, are difficult to detect and observe, and often occur at naturally low densities (Balme et al. 2009).

Within the African large carnivore guild, the majority of publications that employ camera trapping skew towards African leopards *Panthera pardus* (e.g. du Preez et al. 2014; Braczkowski et al. 2016). Historically, research on hyenas has generally been dominated by questions in behavioral ecology, with camera trapping studies only recently gaining traction (Fig. 1). Long-term hyena research projects have mostly occurred in protected areas where the animals are readily observable and, therefore, conducive for behavioral studies (Smith et al. 2017). Among the hyenas, spotted hyenas *Crocuta crocuta* have been the main focus of published literature, with studies of aardwolves *Proteles cristatus*, brown hyenas *Hyaena brunnea*, and striped hyenas *Hyaena hyaena* being scarcer.
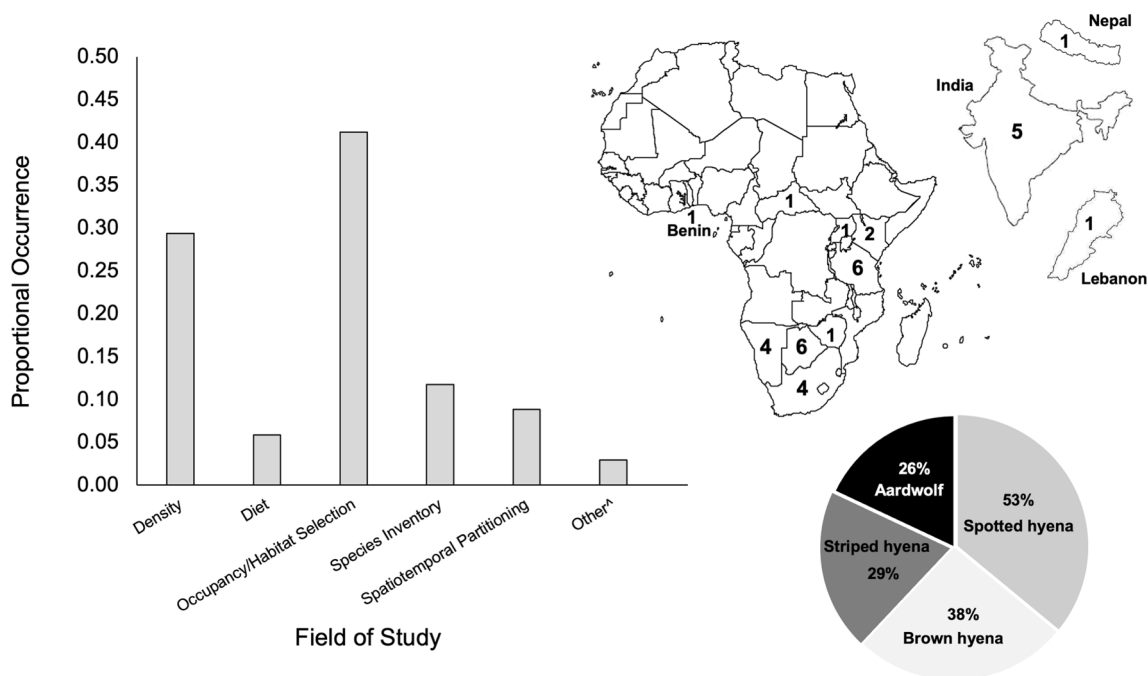
Fig. 1 A literature review of 34 studies (from 2007 to 2020) recovered on Google Scholar showing the hyena species, countries, and research topics encompassing the use of remote camera traps (see Supplementary Material 1 for a list of the studies). We limited our search to studies between 1900 and 2020 and to the first ten pages of results. Search terms were as follows: Spotted hyena: camera trap; *Crocuta crocuta*: camera trap; Striped hyena: camera trap; *Hyaena hyaena*: camera trap; Brown hyena: camera trap; *Hyaena brunnea*: camera trap; Aardwolf: camera trap; *Proteles cristata*: camera trap. We removed all duplicates and classified studies into one of six classes. The "Other" category included only one study (Cusack et al. (2017)), which examined animal species identification using deep convolutional neural networks

For the conservation and management of these species, more studies are needed in areas where hyenas cannot be observed directly, making camera traps crucial in understudied ecosystems. Hyenas possess several traits that make them excellent candidates for camera trapping studies. However, these same traits can also pose challenges for data collection, analysis, and interpretation towards answering questions regarding their ecology and conservation.

We reviewed 34 recently published (between 2007 and 2020) camera trap studies of hyenas (see Supplementary Material). Here, we outline the positive and negative aspects of using camera traps to study members of the family *Hyaenidae* and provide a suite of key recommendations on how to optimize their use. Furthermore, we highlight the potential conservation and management implications of further camera trap studies of hyenas and how these may contribute to wildlife conservation and research in Africa and Asia.

Challenges and opportunities

Individual identification

All four hyena species have patterned pelage: they are either spotted (as in the spotted hyena) or striped (as in the aardwolf, brown hyena, and striped hyena). The natural markings on the left and right sides of the body are different for each animal, which makes individuals distinguishable and allows for capture–recapture analyses. Spotted hyenas are born with solid black natal coats; the coat brightens and spots gradually appear around the age of 1 month (Kruuk 1972). Though cubs are difficult to identify due the fairly uniform natal coat, this can still be done based on differences in ear notches, abrasions on the fur, and other incidental markings (Frank et al. 1991). In

aardwolves, stripes are present along their flanks, forequarters, and legs, and spots may be present on the neck (Sliwa 1996; Spagnuolo et al. 2022). Brown hyenas are most readily identified by looking at the stripe patterns along their fore- and hindlegs (Spagnuolo et al. 2022).

Striped hyenas, like aardwolves, have stripes along their flanks and legs and do not have a natal coat (Rieger 1979). In all hyena species, ear notches and facial scars can also be used for individual identification (Thorn et al. 2009; Alam et al. 2015). However, such markings tend to change size and shape over time (Mills 1982) and should ideally only be used as supplementary features for individual identification. In general, the longer fur of aardwolves, brown hyenas, and striped hyenas can make them more difficult to individually identify than spotted hyenas via camera trap (authors' observation). It is, therefore, prudent to include an uncertainty level for identification in population models (ideally one that can be tested and quantified, as in Johansson et al. 2020).

Associating left and right flank images to the same hyena from camera traps is challenging because images are passively collected without control over which individual is photographed, in contrast to active photo identification surveys where individuals are photographed from both sides. The spotted hyena's propensity to aggregate in groups, perform scent-marking behaviors, and closely investigate and manipulate or destroy unprotected camera traps with their jaws (authors' observation) poses serious practical challenges. In photographs captured during such social activities, it becomes extremely difficult to keep track of specific individuals and assign two flank patterns to the same hyena, especially away from places that the hyenas regularly visit and can be repeatedly captured at (e.g. communal dens or large carcasses). In addition, hyenas regularly rest in puddles (authors' observation), which can discolor and obscure their unique pelage patterns. Lastly, the spots on a spotted hyena's coat tend to fade with age (Frank 1986), which can pose difficulties for long-term studies unless the photographs are of high quality. Accordingly, there are potential context- and species-specific inaccuracies that may influence accurate individual identification and, therefore, population estimates.

Because hyenas are patterned asymmetrically, it is possible to use both complete (double flank) and partial (single flank) identities. When using single flanks, identities can be assigned by identifying individuals separately based on the available flank profiles (right and left) and later selecting the flank profile with the highest number of individuals identified for the analysis (Kalle et al. 2011). In long-term studies using a single flank approach, it is advisable to use a cut-off date (e.g. 1 year) after which there is a comparison of the number of left and right flank shots and the side with a larger sample size is henceforth chosen for all analyses for the project. This allows for the largest possible sample size up to a time limit and avoids the possibility that the flank with more photographs is discarded, which an a priori decision might induce. However, it has been suggested that single flank approaches lead to a loss of precision and an introduction of bias (Meredith 2017; Augustine et al. 2018; Petersen et al. 2019). It is possible to avoid these issues with the use of spatial partial identity models, which can probabilistically resolve the complete identity of single flank samples or photographs that are too blurry to identify using Bayesian techniques (Augustine et al. 2018; Davis et al. 2020).

The decision to use a single flank or double flank approach for hyenas can also depend on the propensity of the animals to aggregate in large groups. For studies in high density areas where hyenas generally aggregate in larger groups (e.g. for many spotted hyena populations), we recommend using only a single flank to identify individuals (Fig. 2). Using the double flank method in such populations may cause mismatches of left and right flank patterns, and, therefore, possibly cause inaccuracies in capture–recapture analyses. The less social hyena species forage alone more often than spotted hyenas (Mills 1982; Bothma and Walker 1999; Watts and Holekamp 2007) and using two flanks for each individual is more suitable. However, in study areas where the less social hyena species regularly forage in

Fig. 2 Camera trap images of the same individual spotted hyena taken at two separate camera trap stations in the Lake Mburo National Park, Uganda, in 2018 (author provided), showing identifiable spot patterns on the right flank
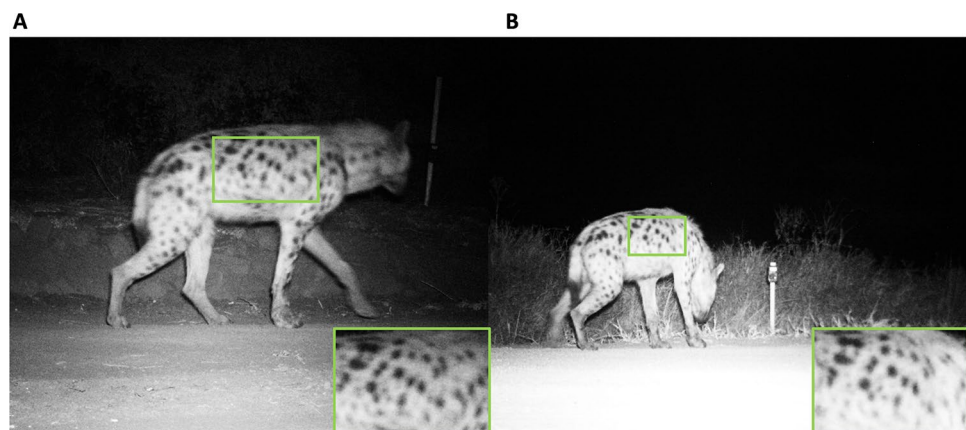
groups or dyads, it is also prudent to use a single flank (e.g. for striped hyenas: Harihar et al. 2010).

Sexual dimorphism

Of the four species in the family *Hyaenidae,* only the spotted hyena has masculinized external female genitalia (termed a pseudopenis) that is accompanied by a pseudoscrotum (Frank et al. 1990; Cunha et al. 2014). Along with minimal sexual dimorphism (Frank et al. 1990), this makes assigning sex to individual spotted hyenas difficult using camera traps (Davis et al. 2018). Aardwolves, brown hyenas, and striped hyenas also exhibit limited sexual dimorphism (Mills 1990; Van Jaarsweld et al. 1995; Wagner et al. 2008), and their long fur makes it difficult to view their external genitalia (Tichon et al. 2017; Hardouin et al. 2021). An inability to sex hyenas from camera trap images has ramifications for both density and occupancy studies. In spotted hyenas, adult females and adult immigrant males differ in their spatial patterning, with males ranging further from and within clan territories (Boydston et al. 2001). The difficulty of identifying sex influences the scale parameter (σ) in camera trap-based density estimation studies and also prevents an estimation of sex ratio (ψ sex), which is an indicator of population health (Holekamp and Smale 1995; Braczkowski et al. 2020). Space use and ranging patterns either do not vary with sex in the other three hyena species, or the differences were deemed non-significant (Wagner et al. 2007; Brekelmans 2012; Edwards et al. 2020). Within our review of camera trapping studies, only one (Hardouin et al. 2021) derived density estimates based on sex, and only for aardwolves.

Despite the apparent lack of sexual dimorphism in hyenas, there are ways to accurately sex them under certain circumstances. In male spotted hyenas, an erect penis has a pointed glans (Fig. 3A). In females, when the pseudopenis is erect, the glans is rounded (Fig. 3B). Therefore, if a camera trap image has a hyena with an erect or semi-erect phallus, one is able to assign a sex. Furthermore, the structure and shape of the pseudopenis changes post-parturition: the female spotted hyena develops a striking patch of pink scar tissue on the back of the phallus, which becomes saggy (Fig. 3C; Frank and Glickman 1994). Moreover, in all hyena species, post-parturition females tend to have pendulous teats due to lactation and suckling which can suffice to distinguish the sexes on camera trap images (Fig. 3D; Kent and Hill 2013; Davidson et al. 2019; Tichon et al. 2020). Regardless, it must be noted that researchers using camera traps are unlikely to be able to sex the majority of individual hyenas with certainty.

Finally, there are alternative approaches that can be used to estimate hyena densities when mark-recapture approaches are unsuitable. For example, camera-based methods that use distance sampling (Howe et al. 2017) and random encounter methods (Cusack et al. 2015) can produce density estimates for carnivores with less individually discernible features, such as lions. Occupancy studies can also be used as proxies for population status without the need for quantified density or abundance estimates, which makes individual or sex-specific identification unnecessary (Schuette et al. 2013). If sex is to be included as a variable in camera trap studies of hyenas, we urge researchers to use it only when sex can be determined unequivocally to avoid accruing errors in datasets and models (Johansson et al. 2020).

Social systems

Hyenas have unusual social systems when compared to other carnivores. Spotted hyenas live in clans that can range in size from fewer than 10 to more than 130 members. Clans are fission–fusion societies in which individuals can aggregate into large groups or be alone (Smith et al. 2008). Brown hyenas also live in clans, though these tend to be smaller than those of the spotted hyena, and adult males may be resident in a clan or nomadic (Knowles
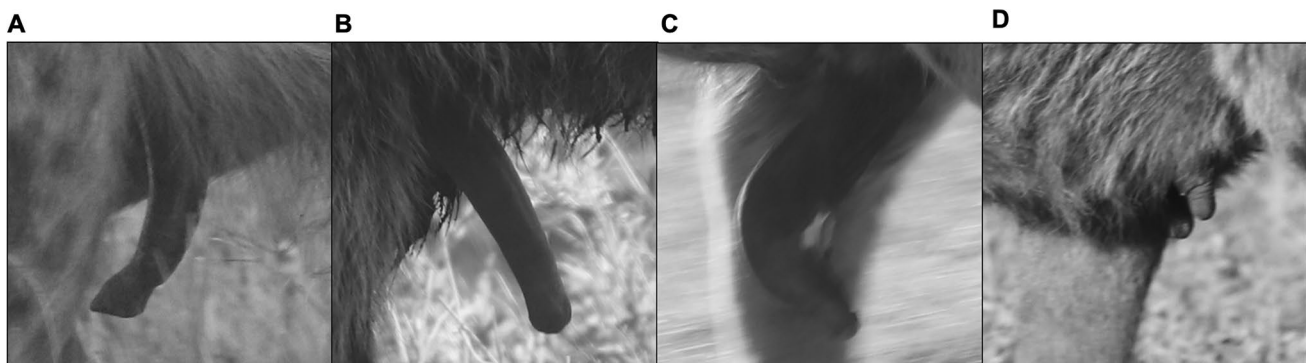

Fig. 3 Camera trap images of four individual spotted hyenas taken at three separate camera trap stations at an undisclosed location in Kenya in 2016 (author provided), showing identifiable secondary sex characteristics: **A** the male penis, **B** the young female pseudopenis, **C** the female pseudopenis post-parturition, and **D** visible teats on a female due to lactation and suckling

et al. 2009; Spagnuolo et al. 2022). Aardwolves live in socially (but not sexually) monogamous pairs (Richardson 1987). Striped hyenas are incipiently social and form small, stable, polyandrous groups (Wagner et al. 2008). However, they have a degree of flexibility in their sociality that has been suggested to depend on carrion availability (Califf et al. 2020; Tichon et al. 2020). In contrast to solitary carnivores such as the leopard, these unique and plastic social systems pose problems with estimating spatial scale parameters, non-independence of detections, and the application of the same methods across species ranges (Foster and Harmsen 2012). Densities of highly social species such as the spotted hyena may also be overestimated in camera trap studies, which is counterproductive for conservation and management efforts (Treves et al. 2010; Cusack et al. 2015). Capture probability can be modeled as a function of social parameters such as sex and then added to a complete density model later in the analysis (Foster and Harmsen 2012). Clan and/or territory sizes in a study area should also be included as covariates that may influence capture probability, as seen in other camera trap studies of ungulates (Massei et al. 2018; Palmer et al. 2018). Clan size can be estimated by assessing the gradual increase (and asymptotic stagnation) in the number of different hyenas detected in a territory (Stratford et al. 2020). Territory size can be estimate using minimum convex polygons or kernel densities (Nilsen et al. 2008).

As long as the aforementioned issues are addressed, concurrent density estimates of hyenas and other carnivores at a single study site can be obtained through camera trapping. Owing to their social complexity and abundance, the number of spotted hyena detections on camera traps is often higher than the number for sympatric carnivores (Rich et al. 2017a, b; Loveridge et al. 2020). This high detectability even in studies where hyenas were "bycatch" augurs well for biologists who may focus on other carnivores but want to provide densities for hyenas (O'Brien and Kinnaird 2011). In areas where hyenas occur at low or moderate densities, camera trap stations can still be spaced a standard distance apart (e.g. ~ 2 km) to provide valuable baseline status estimates in less optimal habitats or at the edge of species' ranges (Hardouin et al. 2021). Indeed, the first camera trapping study to provide density estimates for aardwolves used a multi-species approach (Msuha 2009). In studies where density estimates are not possible to produce due to a lack of recaptures, point observations can provide evidence of the hyena presence in areas where they were previously not known to exist (Maurya et al. 2018). Single observations and the presence/absence studies along the edges of known hyena ranges can improve distribution records and provide valuable data on long-term trends on local extinctions and recolonization by hyenas (Spencer et al. 2020).

Outlook

We contend that the scope for camera trap studies of hyenas is large and that they facilitate updated, accurate range maps and a better understanding of their ecology in areas where hyenas cannot be directly observed (Fig. 1). IUCN Red List conservation status assessments are based on global range and population estimates, which in the case of hyenas, are impossible to accurately develop without camera traps (Gupta et al. 2009). Newer techniques that couple camera trapping with machine learning have become more popular (Tabak et al. 2019), but due to the challenges we raised above, they may be more difficult to use with hyenas. In recognition of this, other methods can be applied, e.g. citizen science efforts such as the Hyaena Distribution Mapping Project which involved trained experts (Killea 2020).

Hyenas are widespread in habitats that are harder to monitor than the open areas of the Mara-Serengeti ecosystem. For example, a camera trap survey in Gabon's Haut-Ogooue province (Bohm 2015) provided baseline abundance estimates for spotted hyenas after several decades of presumed local extinction. Another camera trap survey detected a spotted hyena population and demonstrated the importance of Odzala-Kokoua National Park, Republic of Congo, in the species' conservation in Central Africa (Henschel et al. 2014). In Namibia, a camera trap survey in a fenced system recorded the highest-density brown hyena population known to science (Edwards et al. 2019). Edwards' study highlights the potential for camera traps to detect the effects of fences and closed systems on socio-spatial behavior in hyenas and other carnivores. Camera traps were also used to provide a thorough analysis of social networks, clan size, density, and other features of a spotted hyena population in Namibia which would have been impossible to monitor using direct observations (Stratford et al. 2020). In Nepal, camera traps were used to provide the first-ever record of an active striped hyena den in the country (Khanal et al. 2017). A camera trap study in Israel also suggested that striped hyenas, which were traditionally been described as strictly solitary, are in fact more social than previously thought (Tichon et al. 2020). Novel findings via camera trapping may lead to the documentation of range extensions and ostensibly allow for better conservation outcomes for this misunderstood and declining family. We encourage the use of camera traps for studying hyenas based on a sound understanding of their unique traits, which provide both challenges and opportunities for ongoing research on their distribution, abundance, and conservation.

Declarations

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