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REVIEW

# Room to roam for African lions *Panthera leo*: a review of the key drivers of lion habitat use and implications for conservation

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## ABSTRACT

1. Globally, large terrestrial carnivores (Carnivora) have suffered precipitous declines in population and range. Today, they must persist in increasingly isolated natural habitat patches within a human-dominated matrix. Effective conservation aimed at supporting carnivores in such landscapes requires species-specific understanding of habitat requirements.
2. We present results from a review of the published literature to assess the current state of knowledge regarding habitat preferences of the African lion *Panthera leo*, with the aim of identifying common drivers of habitat use across contexts.
3. Using the Web of Science, we identified 154 usable articles and extracted information relating to study topic, location, habitats described, land-use type, and any documented habitat preferences.
4. Only 31 studies documented evidence of habitat use, and collectively, they suggested that preferences for specific habitat types were varied and context-specific. The importance of prey abundance and proximity to water was highlighted in multiple studies. Anthropogenic factors interfered with expected patterns of habitat use. There was evident bias in study locations: 83% of the habitat-use studies were based in only three countries, and 70% were focussed on protected or managed areas.
5. Our synthesis suggests that lions demonstrate behavioural plasticity in habitat use in response to anthropogenic pressures. To understand the limits of this plasticity and to manage Africa's changing landscapes effectively for roaming lions, future research should be focussed on analysis of habitat use outside protected areas, taking into account gradients of distance to water, prey abundance, and anthropogenic risk.

## INTRODUCTION

Over the past century, humans have altered the world's ecosystems more severely than during any other period of history, and there is overwhelming evidence that human impacts are accelerating (Steffen et al. 2015). Globally, pervasive land-cover change has caused declines in biodiversity through the loss, modification, and fragmentation of natural habitat (Foley et al. 2005, IPBES

2019). Consequently, the number of species currently threatened with extinction has reached unprecedented levels (Díaz et al. 2019).

Biological characteristics, such as large body size, slow reproductive rate, and low population density, make large terrestrial carnivores (Carnivora) particularly vulnerable to habitat fragmentation (McKinney 1997, Keinath et al. 2017). Large carnivores play vital ecological roles as apex predators (Estes et al. 2011, Ripple et al. 2014); thus, their extirpation may have cascading effects on ecosystem structure and functioning. Due to their considerable human–wildlife conflict potential and significant spatial requirements, large carnivores feature prominently in many global conservation projects and policies, and the general causes of their declines are well recognised (Ripple et al. 2014, Trouwborst et al. 2017). However, this understanding has not always translated into adequate conservation action (Ripple et al. 2016).

The African lion *Panthera leo* exemplifies the challenges of conserving top predators. Lions have suffered precipitous population declines in the last century and now occupy only 8% of their historic range (Bauer et al. 2016). Protected areas (PAs), whether large tracts of wilderness or small fenced reserves, are crucial to the long-term survival of lions (Packer et al. 2013, Lindsey et al. 2017). However, approximately 44% of their remaining range lies outside of PAs (IUCN 2018a). Hence, lion conservation strategies must be adaptive to a range of contexts, across a wide mosaic of different land-use and habitat types. To determine the extent to which lions can adapt to habitat modification, and which conservation actions can facilitate this process, it is necessary to understand how lions use existing habitats throughout their remaining range.

Habitat describes the physical nature (biotic and abiotic) of a location of interest (Kearney 2006), referring, for example, to vegetation, climate, and food resources (Gaillard et al. 2010). Habitat use and selection by a species may vary within a range of suitable habitats, based on the quality of resources such as forage, water, and shelter (Hall et al. 1997). Habitat selection is a hierarchical process and inherently scale-dependent (Mayor et al. 2009). At each scale, determinants of habitat selection may differ (Gaillard et al. 2010). Home range selection decisions may be driven by interspecific and intraspecific competition (Rich et al. 2012, Vanak et al. 2013). At a finer scale, habitat selection may be centred on the availability and abundance of resources (Hopcraft et al. 2005, Mueller et al. 2008).

Lions occupy a broad range of biomes and can be found throughout most of sub-Saharan Africa (Bauer et al. 2016), suggesting high tolerance to habitat variation and quality. However, lion ecology and behaviour is shaped at finer spatial scales by interactions between lions and habitat, prey, and people (Patterson 2007). Current understanding of lion habitat selection inside PAs centres on two main hypotheses: the prey abundance hypothesis and the prey catchability hypothesis (Davidson et al. 2012). The prey abundance hypothesis states that habitats are selected to include the highest numbers of prey and that home range size is inversely correlated with prey density (Spong 2002, Davidson et al. 2012). The prey catchability hypothesis proposes that lions select habitats based on attributes that increase hunting efficiency (Hopcraft et al. 2005), e.g. vegetation cover and topography (Hebblewhite et al. 2005). The two hypotheses are not mutually exclusive, and habitat selection by lions is likely to be driven by a combination of prey density and hunting efficiency.

Outside of PAs, anthropogenic pressures can modify habitat use, forcing carnivores into lower quality habitats (Knopff et al. 2014) and confounding patterns expected from the prey-based hypotheses (Valeix et al. 2012). With the rapid expansion of human activities into remaining natural habitats throughout the African continent (Oakleaf et al. 2015), quantifying the consequences for lion habitat use is crucial for developing effective, spatially targeted lion conservation strategies.

We present the results of a literature review to identify common drivers of lion habitat use across contexts. In particular, we aimed to: 1) extract information relating to ecological and anthropogenic attributes of habitats associated with lions, and standardise these factors to quantify their relative importance; 2) use these attributes to develop a conceptual framework for assessing habitat suitability for lions; and 3) critically reflect on biases, gaps and uncertainties in the data that hinder our ability to predict habitat suitability for lions in increasingly human-dominated landscapes.

## METHODS

### Literature search

We conducted our literature search using the Web of Science, which returns articles based on a search of the title, abstract, and key words. We performed our search on 14 October 2019, using the terms *Panthera leo* OR African lion AND habitat OR landscape OR land use, with no specified time span. We first screened articles for relevance based on titles and abstracts and then read in full all articles still considered relevant for our study aims (Appendix S1; Moher et al. 2009). We only included articles that referred to the African lion *Panthera leo*, included a primary empirical observation of lion presence (i.e. not from other literature or modelling), and in which estimates of lion presence could be linked to metrics of habitat in a spatially explicit manner.

For articles presenting continent-wide assessments, we examined the source of the data. If the data were collected by the authors themselves, the article was included as a primary observation (e.g. Packer et al. (2013) provided lion densities for a variety of PAs based on authors' contributions). Articles were included if their focus was on another species, but they documented lion presence with data or observations (e.g. Balme et al. 2017). Articles were also included where there was unequivocal qualitative evidence of lion presence ($n = 6$); for example, Chizzola et al. (2018) compared differences in prey behaviour and stress levels on reserves with and without lions. Articles were excluded where the land-use type of the study area was unclear and could not be determined, and where geographic coordinates for the study area were not provided and the location could not be found on Google Earth.

## Data extraction and analyses

From the final set of articles, we extracted data on study site locations, habitat types present, and any documented habitat preferences. We extracted contextual information, including details of: main study topic, methods used to document lion presence, land use in the study area, and which environmental factors were included in models (e.g. distance to water, vegetation cover, prey biomass). We extracted the geographic coordinates provided in the article, where possible. If this was not possible, we used Google Earth to identify locations based on the names of the study areas.

For the purpose of this review, we defined habitat type as any named land-cover or vegetation type extracted for each study site. Habitat type was typically stated in the 'Study Area' section of the article, which described the landscape in a wider sense rather than fine-scale information on where lions were located. We grouped habitat descriptors into broad habitat types using the International Geosphere-Biosphere Programme classification system mapped by the Moderate Resolution Imaging Spectroradiometer land-cover product MCD12Q1 (MODIS MCD12Q1: IGBP; Friedl & Sulla-Menashe 2019; Appendix S2). For example, an article describing the study area as short grass plains and open deciduous woodland was coded as 'Grassland' and 'Woodland'. To identify the most commonly occurring habitat types, articles were grouped by location (e.g. Hwange National Park, Zimbabwe) and the number of distinct habitats described for each location was recorded. As some articles included more than one study site, and some articles pertained to the same study site, the sample size for the habitat analysis was not equal to the number of articles included in the review.

To fill data gaps for articles that did not describe the habitat types present at their study site ($n = 29$), we extracted land-cover type for each study from MODIS MCD12Q: IGBP, including all habitats mapped within a buffer around the study site coordinates. Three buffers were tested based on minimum lion home range size, and an 8-km buffer was considered broadly sufficient for capturing habitat type in each study area (Appendix S3). To assess differences between reported and extracted habitat, data from those articles that had stated habitat type were compared with habitat data for the same locations extracted from the MODIS layer (Appendix S3).

To examine the anthropogenic pressures being exerted on lion habitats, we used the Human Footprint Index, which quantifies the cumulative impact of built environments, intensive agriculture, pasture lands, human population density, night-time lights, roads, railways, and navigable waterways (Venter et al. 2016a, b). Results are provided on a 0-50 scale, with zero representing no measurable anthropogenic pressure. We overlaid the most recent lion range map provided by the International Union for Conservation of Nature (IUCN; Bauer et al. 2016) with the Human Footprint Index map to determine the number of pixels within the African lion's range that are subject to various levels of anthropogenic pressure.

For articles that specifically covered habitat use or selection, we used a vote-counting procedure to determine which habitat factors were consistent correlates of lion habitat use. This procedure involved counting the number of studies with significant positive results, significant negative results, and non-significant results. We acknowledge the constraints of this method in failing to account for effect size and sample size (Bushman & Wang 2009), and therefore, we simply aimed to provide a descriptive summation and narrative for patterns and conflicts and to highlight the relative importance of variables contributing to lion habitat selection. Based on the most commonly observed patterns, we created a conceptual framework showing the expected interactions between drivers of habitat use and the key habitat preferences of lions. We also used this framework to highlight several factors that are likely to be important but for which data are currently lacking.

To assess biases in the literature, we explored spatial representativeness using plots of occurrence in the literature of countries within the lion geographic range and the land-use types covered by the study areas. All data exploration and analysis was implemented in R statistical software version 3.6.3 (R Core Team 2020).

# RESULTS

## Literature search

The search in the Web of Science returned 337 articles. After filtering by title and abstract, 206 articles were retained and read in full. These were assessed against the inclusion criteria, and data were extracted from 154 articles covering 128 independent study sites (Appendix S1 and S4). Articles identified as relevant were published between 1997 and 2019, and 49% of these were published in the last five years. We identified nine broad study themes based on aims and key words (Appendix S5). The dominant topic was focussed on species other than the lion, but documented lion presence (29% of the 154 articles), followed by studies on human–wildlife conflict (21%) and habitat use (15%). Study foci for the habitat-use category included habitat use, selection, quality, and occupancy (Appendix S5).

## Habitat use and selection

Grassland was the dominant habitat type across study sites, occurring at 88% of locations (112 of the 128 study locations represented in the 154 articles) followed by woodland (62%), shrubland (60%) and savanna (52%; Fig. 1). Habitats created by humans (cropland, mosaic, and urban) were present at 37 study sites (29%). However, the majoritiy of incidences of these human-modified habitats occurred where data had been extracted from the MODIS land-cover product (89% of human-created habitat locations) rather than from study area descriptions. Based on the Human Footprint Index, 31% of the land within the geographic range of the African lion is under high or very high anthropogenic pressure (Human Footprint Index ≥6; Venter et al. 2016b), while 28% remains under no or low anthropogenic pressure (Human Footprint Index 0–2).

Landscapes in which lions occurred were most often composed of three or four habitat types (59% of the study locations), compared with 14% locations with only one habitat type (50% of which were grassland). When considering only the four most common habitat types, the most frequently observed habitat composition ($n$ = 24) encompassed grassland, savanna, woodland, and shrubland (Fig. 2). This summary does not account for spatial scale; studies conducted in larger National Parks or at broader spatial extents may encompass a wider range of habitats. However, it may also be the case that studies at broader

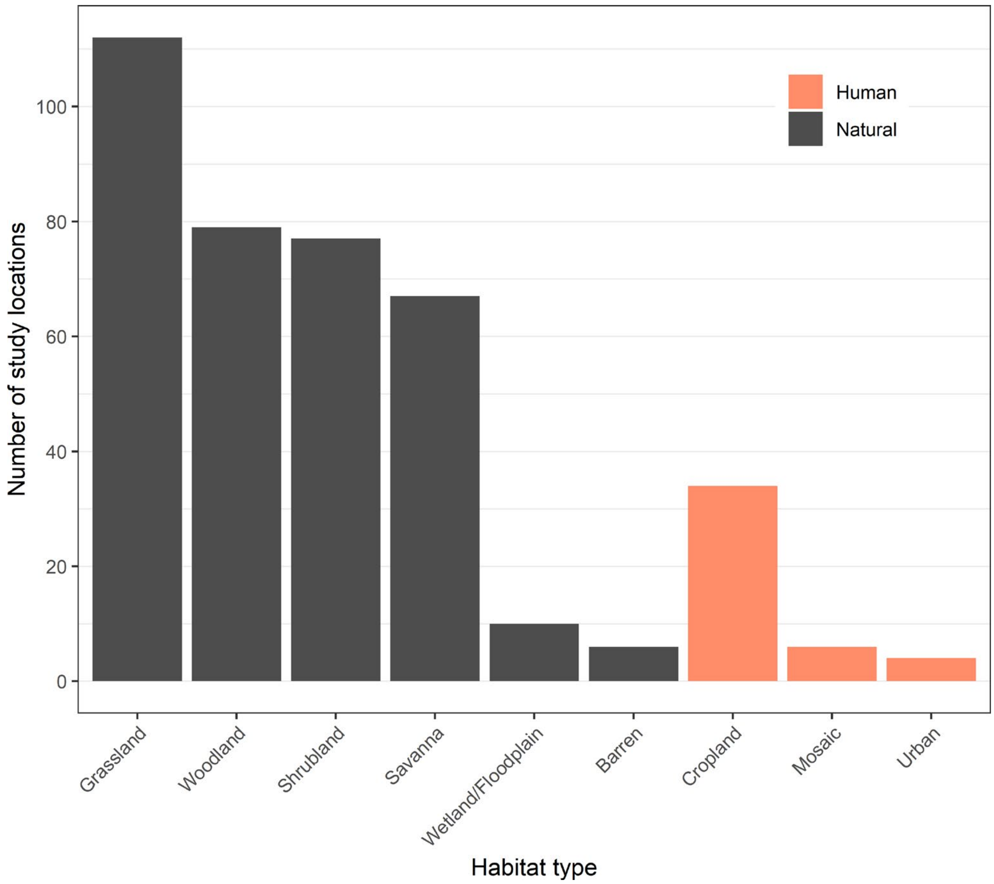


**Fig. 1.** Habitat types occurring at 128 study locations represented in 154 articles included in the review of African lion *Panthera leo* habitat use. Colours indicate whether the habitat type is naturally occurring or human-created. Study locations including several habitat types are represented multiple times in the graph: in total, the 128 study locations included 395 habitat type data points.

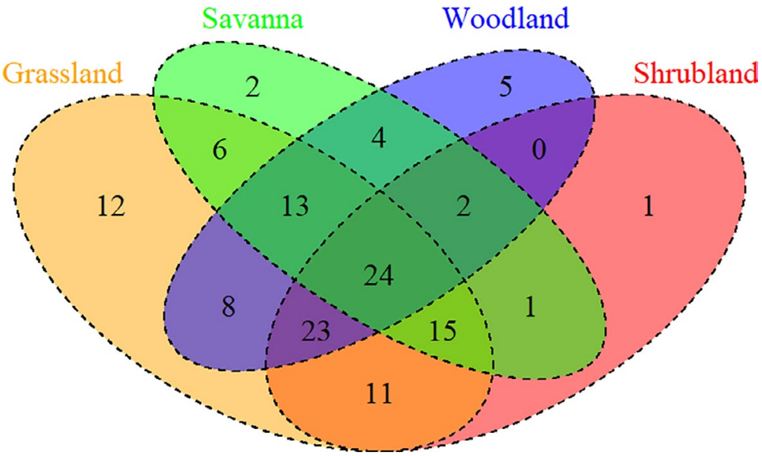


**Fig. 2.** Diagram representing the co-occurrence of the four most common habitat types at study sites used for African lion *Panthera leo* research. Numbers indicate the number of study locations containing that habitat composition.

spatial extents describe habitats in a broader sense, while smaller site descriptions contain more specific detail on local habitat types.

We present our findings with a note of caution. The majority of articles described habitat at the scale of the study area in general terms, with only few spatially explicit details on lion observations within their study area. With the current state of evidence, it was not possible to determine whether lions used all documented habitats.

More detailed evidence regarding lion habitat use was extracted from the 23 articles that were focussed on habitat use and selection, and from a further eight articles, in which the main focus was not habitat use but which documented evidence of lion habitat preference (Appendix S6; Table 1). Studies were split into those that were conducted solely inside PAs and those that considered multiple land-use types (Table 1). Mixed land-use studies typically contained a combination of protected and unprotected areas, but only two of these made a direct comparison of habitat use inside vs outside the PA (Appendix S6). There was evidence for habitat use being highly variable and context-dependent. Of studies that considered habitat types inside PAs, 45% found that lions selected for open habitat such as grassland, while 18% found a preference for woodland. Some studies found that habitat use varied seasonally or based on behaviour

**Table 1.** Summary of environmental and anthropogenic variables related to habitat use of lions *Panthera leo*, split by articles that were focussed only on protected areas and those that considered multiple land-use types. Only variables measured in >2 articles are included in the table. Measures of habitat use included occupancy, density and selection. See Appendix S6 for details of each article. *n* = the number of articles in which the variable was examined; *n* positive/negative = the number of articles that found a significant positive or negative association between the variable and lion habitat use; % = percentage of articles in which the variable was related to habitat use in some way, including positive/negative associations and more complex interactions; n/a = not applicable because the variable is categorical

| | Protected areas only (*n* = 16) | | | | Mixed land use (*n* = 15) | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | *n* | *n* positive | *n* negative | % | *n* | *n* positive | *n* negative | % |
| Environmental | | | | | | | | |
| Habitat type | 11 | n/a | n/a | 100% | 6 | n/a | n/a | 67% |
| Distance to water | 8 | 0 | 7 | 88% | 9 | 1 | 3 | 33% |
| Prey abundance (density/biomass) | 6 | 4 | 0 | 67% | 3 | 2 | 0 | 67% |
| Elevation | 3 | 0 | 2 | 67% | 3 | 0 | 1 | 33% |
| Precipitation | 2 | 1 | 0 | 50% | 3 | 2 | 0 | 100% |
| Vegetation cover | 4 | 1* | * | 50%* | 7 | * | 1* | 29%* |
| Slope | 3 | 0 | 1 | 33% | 3 | 0 | 0 | 0% |
| Anthropogenic | | | | | | | | |
| Land use | n/a | n/a | n/a | n/a | 9 | n/a | n/a | 100% |
| Distance to settlements/buildings | 3 | * | * | 33%* | 11 | 3* | 2* | 64%* |
| Human density | 1 | 0 | 0 | 0% | 4 | 0 | 1 | 25% |

*Often varied based on other factors.

(e.g. selecting grassland at the home range scale but hunting in dense thickets). Lions typically selected habitats with high prey abundance, both inside PAs and in the wider landscape (Table 1). In PAs, lions were often found to use habitats in close proximity to water (Table 1). However, in studies that considered distance to water across a mixed-use landscape, only 33% found an association with lion presence (Table 1). In response to anthropogenic variables, lions appeared to adapt their behaviour and habitat use. This occurred at both a land-use scale, with lions avoiding pastoral areas, increasing their use of closed habitats and avoiding water when outside of PAs; and at a temporal scale, as lions exhibited increased avoidance of anthropogenic habitats during the day, when human activity was high (Appendix S6).

There was considerable variation in sample size between studies: some presented data for only four individual lions, while other long-term projects had data for as many as 84 lions (Appendix S6). However, these differences in sample size did not appear to be driving observed patterns.

We used the literature to construct a conceptual framework, presenting likely lion habitat preferences and links between

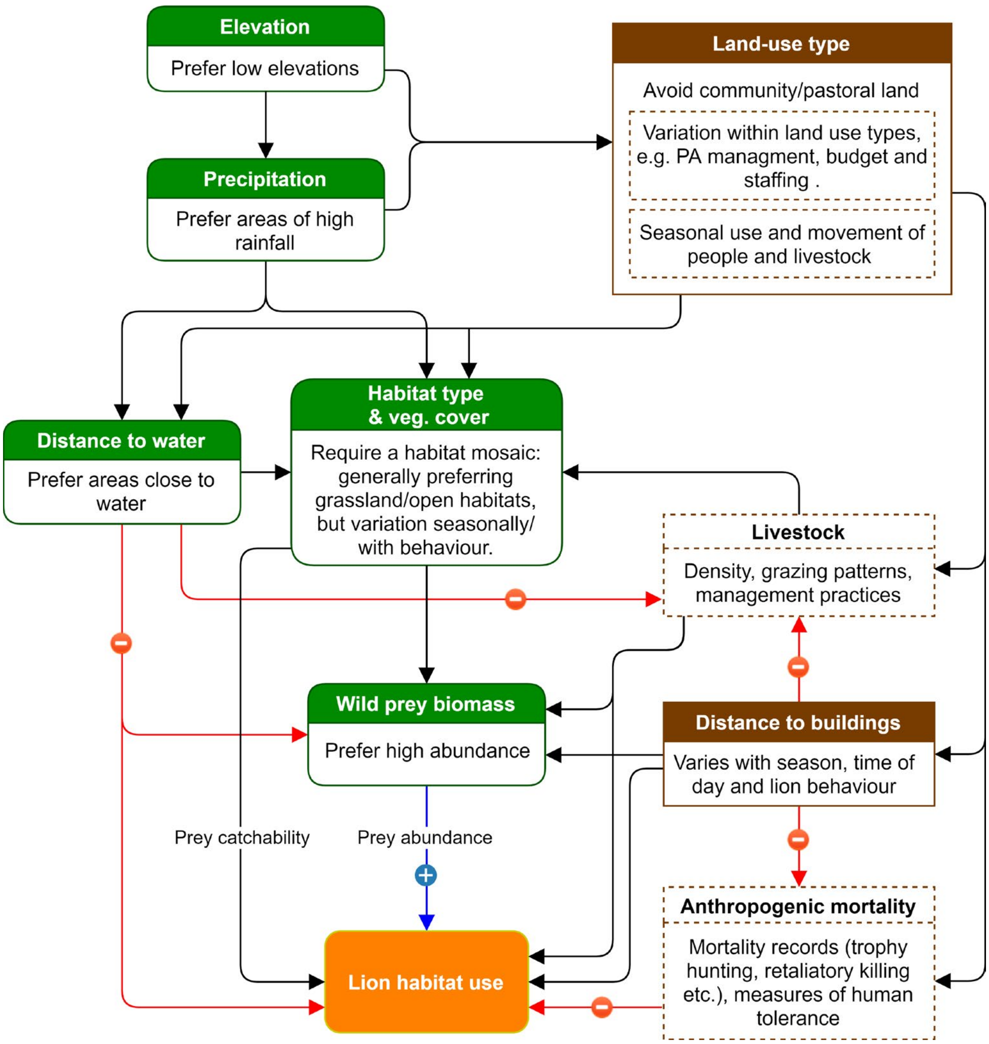


**Fig. 3.** Conceptual framework of the direct and indirect pathways through which environmental and anthropogenic variables affect African lion *Panthera leo* habitat use. Boxes with rounded corners represent key environmental drivers and expected habitat preferences of lions when free of anthropogenic pressures. Boxes with straight edges show anthropogenic factors and pathways through which they may interact with environmental drivers and alter lion habitat use. Boxes with dashed outlines indicate factors that we expect to have an impact on habitat use but which were studied in ≤2 papers, highlighting knowledge gaps that should be the focus of future research. Arrows indicate directions of main effects; e.g. distance to water influences wild prey biomass. For key quantitative drivers where dominant effect directions could be hypothesised, arrows with a '-' symbol represent a negative association and arrows with a '+' represent a positive association. However, we highlight that these relationships may vary with context and that there is a hierarchy of drivers that are too complex to be captured fully in this framework. For example, some of these interactions may vary temporally or with lion behaviour.

the key components underpinning lion habitat use (Fig. 3). The most consistently observed habitat preferences were for areas of high prey abundance close to water. Land-use type was also important, with lions typically avoiding unprotected community lands used for agro-pastoralism and human settlement (Appendix S6). However, of other anthropogenic variables, only distance to settlements/buildings was examined frequently in the literature, and there was considerable variation depending on season, time of day, and lion behaviour (Table 1). We identified data gaps for several other anthropogenic drivers, which are likely to modify lion habitat use, but which were measured in only one or two studies (Fig. 3).

## Land use

Land use was grouped into three broad types: PAs, other managed areas, and unprotected areas (Fig. 4). Most study sites contained PAs ($n = 120$ articles), which included National Parks, National Reserves, and private game reserves; 38 articles had study sites that encompassed some form of wildlife-managed area (hunting zones, community land management areas, wildlife-friendly ranches, and buffer zones adjacent to National Parks); and 32 articles (21%) included completely unprotected areas (community and village land, and commercial ranches). Of the 154 articles, 29 included more than one land-use type. Of the 31 articles that documented evidence of habitat use, 29% (9 articles) had study sites that contained unprotected areas (Fig. 4; Appendix S6).

Studies inside PAs primarily used unambiguous detection methods to document lion presence, such as Global Positioning System collars, camera traps, or direct observation of lions (Fig. 4). In contrast, outside PAs it was more common for researchers to use methods such as interviews (28% of articles that included unprotected areas) and records of conflict events, such as livestock depredations or attacks on humans (25% of articles that included unprotected areas; Fig. 4).

## Spatial representativeness

Lions are believed to be resident in 25 African countries (Bauer et al. 2016). Around two thirds ($n = 17$) of these countries were represented in the relevant literature for this review. We also found three articles documenting lion

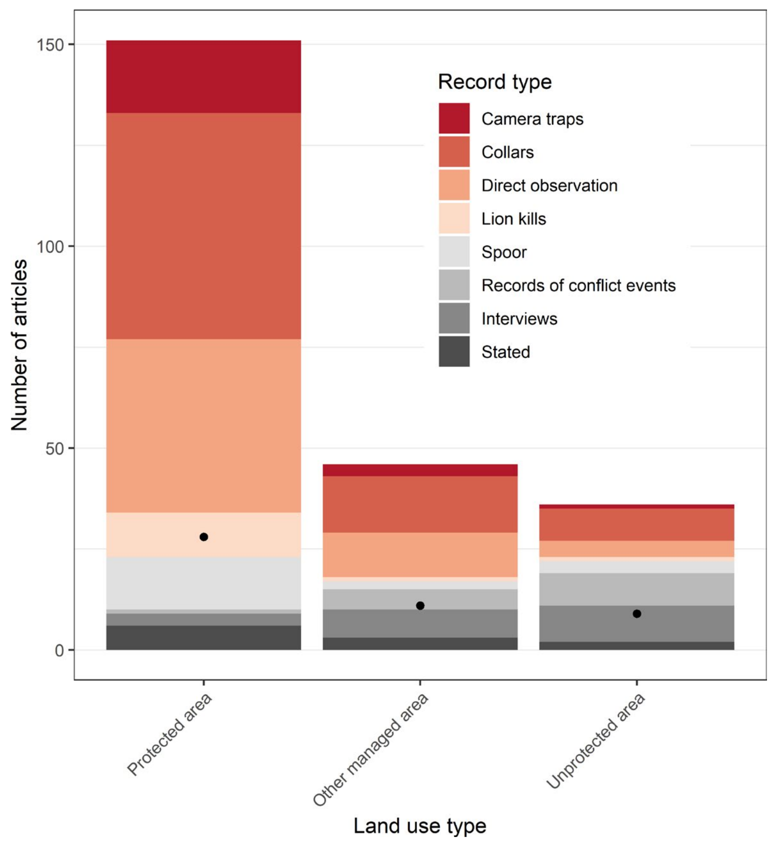


**Fig. 4.** Number of articles on African lions *Panthera leo* inside and outside protected areas, and the methods used to document lion presence. Articles are represented more than once if they included more than one land-use or record type: in total, there are 233 data points. Black dots represent the number of articles that documented evidence of lion habitat use per land-use type (48 data points from 31 articles).

presence in countries where lions are considered extinct or possibly extinct (Ghana and Gabon; Fig. 5). The majority of articles presented data from just four countries (Tanzania, Kenya, South Africa, and Zimbabwe; Fig. 5), which are also among the nine countries that are likely to still contain >1000 lions; the others being Botswana, Mozambique, Zambia, Central African Republic, and possibly Angola (Riggio et al. 2013). Only 4.5% of articles included study sites representing the West and Central African region (Fig. 5). Of the 31 articles that provided data on habitat use, eight had study sites in Tanzania, eight in South Africa, and seven in Zimbabwe (Fig. 5; Appendix S6).

With reference to specific study sites within countries, of the 128 study locations named in the 154 articles, the majority ($n$ = 104) were represented just one or two times in the literature. Hwange National Park and surroundings, in Zimbabwe, and Serengeti National Park, in Tanzania, were notable exceptions, contributing 22 and 18 articles, respectively.

# DISCUSSION

## Habitat use and drivers

Our findings, drawing from the 31 studies that documented evidence of habitat use, indicate that space use and habitat preferences of African lions are highly context- and scale-dependent, with prey abundance and proximity to water being consistent, prominent drivers. African lions, when free from anthropogenic pressures, appear to select open areas, such as grassland and open shrubland (Cristescu et al. 2013, Courbin et al. 2016), probably because these habitats support a higher abundance of their preferred prey species (Spong 2002, Miller et al. 2018). However, when engaged in certain behaviours, such as hunting or dispersal, lions may utilise habitats with increased vegetation cover (Hopcraft et al. 2005, Davidson et al. 2012, Elliot et al. 2014). The importance of varying levels of vegetation cover is supported by our finding that grassland was the most common habitat type present at study sites, but that the majority of locations contained some combination of open and closed habitats (Fig. 2).

Within PAs, proximity to water is a key driver of lion habitat selection (Valeix et al. 2010, Davidson et al. 2012, Abade et al. 2014). In arid and semi-arid landscapes, the distribution of herbivores is largely influenced by the availability of patchily distributed surface water. Lions, therefore, have a greater chance of encountering prey in areas around water sources (Valeix et al. 2010). However, a negative relationship between lion habitat use and distance to water was less often observed in those studies that considered landscapes outside of PAs.

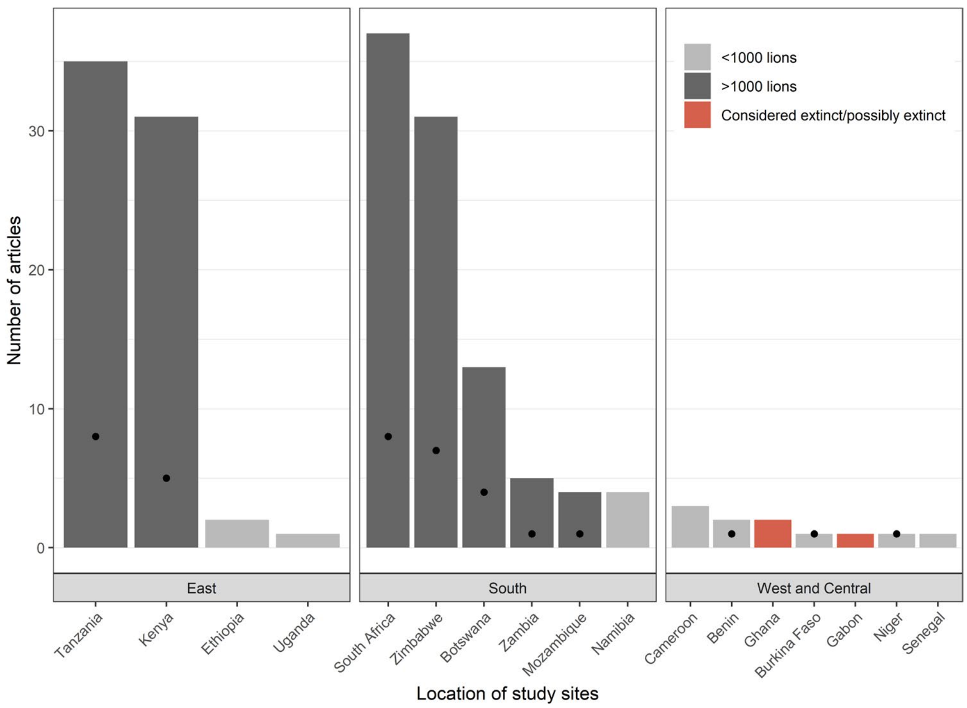


**Fig. 5.** Locations of the study sites in the 154 articles in the review, grouped by country and region of Africa. Colours indicate the estimated size of each country's African lion *Panthera leo* population. Articles with study sites spanning more than one country are represented more than once in the graph: in total, the 154 articles included 174 country data points. Black dots represent the number of articles documenting lion habitat use per country (37 data points from 31 articles).

Anthropogenic pressures alter expected patterns of habitat use, probably due to their effect on feeding behaviour and mortality risk (Mogensen et al. 2015, Loveridge et al. 2017). Compared with lions in areas of low anthropogenic pressure, lions on pastoral lands have been found to occur more frequently in closed habitats, consume prey inside bushes, abandon kills more often, and avoid areas close to water (Schuette et al. 2013, Mogensen et al. 2015, Mkonyi et al. 2018). Where natural prey is depleted due to hunting by humans, displacement by livestock, or seasonal variation in prey abundance, lions may increase their proximity to humans in order to access livestock as secondary prey (Patterson et al. 2004, Valeix et al. 2012). However, when doing so, they are likely to make temporal adjustments to their behaviour to avoid overlap with periods of high human activity (Valeix et al. 2012, Oriol-Cotterill et al. 2015a).

The results of the studies based outside of PAs suggest that hypotheses for habitat use of lions in human-dominated landscapes could be framed around diurnal and seasonal shifts in behaviour to facilitate avoidance of people. To develop these hypotheses, future research should be focussed on temporal variation in habitat use, and researchers should consider a wider range of possible anthropogenic pressures to fill current knowledge and data gaps (Fig. 3).

The behavioural flexibility exhibited by lions may suggest that they have the potential to tolerate increasingly human-dominated environments. However, the use of refuge habitats when in proximity to humans is likely to result in a trade-off between nutritional intake and mortality risk (Oriol-Cotterill et al. 2015b). The fitness consequences of using these suboptimal habitats, abandoning kills, and being displaced from water sources are not yet understood. Indeed, only one study attempted to examine fitness-based measures of habitat quality, finding that lion reproductive success, productivity, and density were often positively correlated with proximity to river confluences and dry-season rainfall (Mosser et al. 2009).

## Data gaps and sampling bias

Our work reveals a surprising lack of robust evidence on the species' use of habitats for large parts of its geographic range and specifically for landscapes dominated by human activities.

The majority of studies were located in only four countries, and furthermore, some locations within countries, such as Hwange National Park and Serengeti National Park, were distinctly overrepresented. In West and Central African counties, which have seen rapid human-driven changes in land use in the past decades (Mallon et al. 2015), the lion is not only genetically distinct but also classified as Critically Endangered (Bertola et al. 2011, Henschel et al. 2014). However, only 4.5% of articles had study sites based in West and Central Africa, a knowledge gap previously highlighted by Henschel et al. (2014).

Thus, our understanding of lion ecology and habitat preferences is based on a few well-known case studies representing a fraction of the species' range. Using this evidence base to develop conservation strategies should be approached with caution, as the literature unequivocally highlights the spatial and temporal complexity of lion–human–environment interactions. Collecting evidence from countries that represent the range of variation in this system should be prioritised in the coming years, in order to develop effective conservation interventions.

Studies were also predominantly conducted inside PAs. Although our Human Footprint Index analysis revealed that some areas of the lion range have yet to suffer severe human impacts, projections suggest a doubling of the human population in sub-Saharan Africa by 2050 (UN 2019) and a tripling of the extent of land converted to human use in Africa in the coming decades (Oakleaf et al. 2015). This makes understanding the use of human-dominated landscapes by lions vital for effective conservation. It was therefore promising to see that, of the studies specifically focussed on habitat use, almost one third contained study sites that encompassed unprotected areas, at least as part of their methodological design.

The observed bias towards PAs may be driven in part by practical constraints on monitoring wildlife outside of PAs. Several articles note that lions in community land can be shy and difficult to locate (Schuette et al. 2013, Mogensen et al. 2015), and some researchers failed to detect any lions outside PAs despite their known presence there, as confirmed by conflict reports (Abade et al. 2019). With the increasing use and development of Global Positioning System collars and camera traps, it may be that we see an increase in studies focussed outside of PAs. Indeed, of the nine habitat-use studies that considered land outside of protected or managed areas, five were published in 2018 or 2019.

However, even within the studies that considered multiple land-use types, the scope of the anthropogenic variables considered was often limited. Most studies were focussed on distance to human structures, using this to infer levels of risk rather than records of actual lion mortality (Loveridge et al. 2017). Furthermore, while most studies consider static land-use types (e.g. PA, community land), lions may respond at finer scales to differences in land management, such as changing numbers of patrol staff (Henschel et al. 2016) and seasonal movement of people and livestock (Schuette et al. 2013). Measures of livestock abundance and distribution were rarely considered, representing a significant data gap in the literature on lion habitat use. One study that did measure livestock presence found a negative association between lion occupancy and the presence of cattle (Everatt et al. 2019).

## The challenge of defining habitats

Terms used to describe habitat types are used inconsistently in the literature, complicating our attempt to standardise habitats across studies and scale up to the wider lion range. Savanna, for example, is described in one study as an area 'dominated by bushlands' (Courbin et al. 2016) and in another as 'dominated by perennial grasses' (O'Brien et al. 2018). While savanna is considered a distinct habitat type characterised by continuous grass cover and widely spaced trees and shrubs (IUCN 2018b), it can encompass a broad spectrum of woody cover transitional between grassland and forest (Sankaran et al. 2004, Parr et al. 2014), making it inherently difficult to define.

Some studies describe habitat using maps created from ground surveys of vegetation composition, soil type, geology, and topography (Davidson et al. 2012, Millspaugh et al. 2015). Others use maps derived from Earth observation products (Elliot et al. 2014, Mkonyi et al. 2018), with land-cover categories and map accuracy differing between products. This can introduce considerable confusion and result in a mismatch between the definitions of habitat classes depending on the product used (Giri et al. 2005).

## Future directions of research

We recommend that future studies of lion habitat use aim to address existing biases by directing research towards less well-studied countries, focussing on landscapes outside of PAs and measuring a wider range of anthropogenic pressures. Our conceptual framework illustrates the key factors that should be considered when assessing habitat suitability for lions. Montgomery et al. (2018) posit that there are five dimensions that determine patterns of human–lion conflict: the lion, the wild prey, the environment, the human, and the livestock. We suggest that these dimensions should also be considered when examining lion habitat use in human-dominated landscapes. At present, there is a significant gap in the literature with regard to the livestock dimension, as well as only limited consideration of human variables, the main focus being on distance to buildings (Fig. 3). Our framework can be used as a starting point to guide future research towards filling these data gaps and disentangling the complex interplay of variables affecting lion habitat use.

It is also important to consider habitat definitions and improve clarity on how these are categorised and mapped. The Land Cover Classification System developed by the Food and Agriculture Organization and the IUCN Habitat Classification Scheme aim to address this problem by providing a standardised system that can be used globally and would allow for comparable research and sampling designs (Di Gregorio & Jansen 2000, IUCN 2018b). However, authors of landscape ecology studies have also called for a move away from categorical land-cover descriptors, towards metrics that represent continuous environmental gradients in resource quality and availability (Manning et al. 2004, Fischer & Lindenmayer 2006). We lend further support to this move, highlighting that Earth observation increasingly allows us to study relevant habitat metrics, such as vegetation structure and productivity, at fine spatial resolutions (Coops & Wulder 2019, Oeser et al. 2020).

Our results highlight that many environmental factors drive lion habitat use via their relationship with prey abundance. We suggest directing research towards understanding the habitat preferences of primary prey species across a gradient of anthropogenic pressure. Given that lions are frequently found in habitat mosaics that include grassland and that the preferred prey species of lion are water-dependent grazers (Hayward & Kerley 2005), managing pressures on grassland habitats is likely to be fundamental for protecting prey populations.

We also encourage a more targeted approach to monitoring lions in relation to water sources. Displacement of wildlife at water sources and competition with livestock for water and forage affects wild herbivore abundance and distribution (Ogutu et al. 2014). Managing water points outside of PAs to provide safe access for both people and wildlife may be a way of increasing landscape suitability for wild prey species and therefore, lions. Water availability will become an increasingly important issue for both wildlife conservation and human well-being as climate and land-use change affect rainfall, surface water supply, and vegetation productivity throughout Africa (de Wit & Stankiewicz 2006, Ogutu et al. 2008).

# CONCLUSIONS

The IUCN Guidelines for the Conservation of Lions state that a key objective is 'to conserve current lion habitat and prey base' (IUCN 2018a). However, without clearly defined targets for the habitat features required by lions, there is little guidance for how to manage landscapes and develop effective intervention measures. Our review reveals a relatively infrequent focus on habitat use amid the extensive catalogue of lion research. The studies that are focussed on habitat use show that under optimal conditions of low anthropogenic pressure and high prey abundance, lions select for open grassland habitats and areas near water. However, lions demonstrate a high degree of flexibility and can adapt their habitat use to improve their security and prey catchability. To target conservation interventions effectively and predict how lions will adapt to changing landscapes, future research should strive for detailed analysis of factors such as distance to water, prey abundance, and anthropogenic risk, in order to determine what makes good lion habitat.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

**Appendix S1**. PRISMA flow diagram of article selection.
**Appendix S2**. Coding of habitat types.
**Appendix S3**. Validation exercise comparing Earth observation data to data extracted from the literature.
**Appendix S4**. Studies included in qualitative synthesis.
**Appendix S5**. Coding of study topics.
**Appendix S6**. Table summary of results for 23 lion habitat use articles, plus a further 8 relevant articles.