Trends and biases in African large carnivore population assessments: Identifying priorities and opportunities from a systematic review of two decades of research

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African large carnivores have undergone significant range and population declines over recent decades. Although conservation planning and the management of threatened species requires accurate assessments of population status and monitoring of trends, there is evidence that biodiversity monitoring may not be evenly distributed or occurring where most needed. Here, we provide the first systematic review of African large carnivore population assessments published over the last two decades (2000-2020), to investigate trends in research effort and identify knowledge gaps. We used generalised linear models (GLMs) and generalised linear mixed models (GLMMs) to identify taxonomic and geographical biases, and investigated biases associated with land use type and author nationality. Research effort was significantly biased towards lion (*Panthera leo*) and against striped hyaena (*Hyaena hyaena*), despite the latter being the species with the widest continental range. African wild dog (*Lycaon pictus*) also exhibited a negative bias in research attention, although this was partly explained by its relatively restricted distribution. The number of country assessments for a species was significantly positively associated with its geographic range in that country. Population assessments were biased towards southern and eastern Africa, particularly South Africa and Kenya. Northern, western, and central Africa were generally under-represented. Most studies were carried out in photographic tourism protected areas under government management, while non-protected and trophy hunting areas received less attention. Outside South Africa, almost half of studies (41%) did not include authors from the study country, suggesting that significant opportunities exist for capacity building in range states. Overall, large parts of Africa remain under-represented in the literature, and opportunities exist for further research on most species and in most countries. We develop recommendations for actions

aimed at overcoming the identified biases and provide researchers, practitioners, and policymakers with priorities to help inform future research and monitoring agendas.

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Abstract

African large carnivores have undergone significant range and population declines over recent decades. Although conservation planning and the management of threatened species requires accurate assessments of population status and monitoring of trends, there is evidence that biodiversity monitoring may not be evenly distributed or occurring where most needed. Here, we provide the first systematic review of African large carnivore population assessments published over the last two decades (2000-2020), to investigate trends in research effort and identify knowledge gaps. We used generalised linear models (GLMs) and generalised linear mixed models (GLMMs) to identify taxonomic and geographical biases, and also investigated biases associated with land use type and author nationality. Research effort was significantly biased towards lion (*Panthera leo*) and against striped hyaena (*Hyaena hyaena*), despite the latter being the species with the widest continental range. African wild dog (*Lycaon pictus*) also exhibited a negative bias in research attention, although this was partly explained by its relatively restricted distribution. The number of country assessments for a species was significantly positively associated with its geographic range in that country. Population assessments were biased towards southern and eastern Africa, particularly South Africa and Kenya. Northern, western, and central Africa were generally under-represented. Most studies were carried out in photographic tourism protected areas under government management, while non-protected and trophy hunting areas received less attention. Outside South Africa, almost half of studies (41%) did not include authors from the study country, suggesting that significant opportunities exist for capacity building in range states. Overall, large parts of Africa remain under-represented in the literature, and opportunities exist for further research on most species and in most countries. We develop recommendations for actions aimed at overcoming the identified biases and provide researchers,

42 practitioners, and policymakers with priorities to help inform future research and monitoring

43 agendas.

Introduction

45 Africa is host to a unique diversity of large carnivore species, including the lion (*Panthera leo*),

46 leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), African wild dog (*Lycaon pictus*),

47 spotted hyaena (*Crocuta crocuta)*, striped hyaena (*Hyaena hyaena*), and brown hyaena

48 (*Parahyaena brunnea*). Nevertheless, large carnivore populations across Africa have undergone

49 rapid declines in recent decades, primarily as a result of habitat loss and fragmentation, loss of

50 prey, and conflict with humans (Brodie et al., 2021; Wolf and Ripple, 2017). As large carnivores

51 can help generate tourism revenue (Hemson et al., 2009), often have strong cultural importance

52 (Dheer et al., 2021), and play a key role in the provision of ecosystem services (Davidson et al.,

53 2019), there are strong practical and intrinsic motivations for the successful conservation of

54 remaining African large carnivore populations.

55 Knowledge of the status and trends of populations is essential for effective conservation

56 management of large carnivores (Elliot and Gopalaswamy, 2016). Information on population

57 status allows practitioners to identify threats, evaluate the effectiveness of interventions,

58 implement adaptive monitoring programmes, and inform policy (Suryawanshi et al., 2019;

59 Witmer, 2005). Indeed, data on large carnivore population status have been used in recent years

60 to inform a wide range of management and policy decisions, including national and regional

61 action plans and conservation strategies (IUCN, 2007; TAWIRI, 2016), range-wide meta-

62 analyses (Weise et al., 2017), international policies (USFWS, 2015), extinction risk assessments

63 (IUCN, 2020), and trophy hunting quota setting (Mweetwa et al., 2018; Packer et al., 2011).

64 Such data have also been employed to identify population strongholds (Riggio et al., 2013) and

65 range-wide conservation priorities (Bauer et al., 2015a), and to inform controversial management

66 practices (Miller and Funston, 2014; Packer et al., 2013).

67 Conversely, lack of data on population status often leads to knowledge gaps being filled by

68 expert opinion (Weise et al., 2017), which can delay or prevent conservation actions (Artelle et

69 al., 2013; Popescu et al., 2016), or lead to inappropriate or harmful management decisions

70 (Darimont et al., 2018; Moqanaki et al., 2018). Successful large carnivore conservation therefore

71 requires reliable population assessments (Braczkowski et al., 2020), ideally from a wide range of

72 geographical and management contexts. However, as a result of often existing at naturally low

73 densities, exhibiting nocturnal and secretive traits, and ranging across large areas, estimating

74 population parameters for large carnivores can be logistically challenging and financially costly

75 (Karanth and Nichols, 2017). Indeed, African carnivore population measures have been argued

76 to be severely lacking (Riggio et al., 2013), and there is evidence that biodiversity monitoring

77 and research as a whole is under-represented in Africa (Di Marco et al., 2017; Martin et al.,

78 2012; Stocks et al., 2008; Velasco et al., 2015).

79 Conservation research also suffers from both taxonomical and geographical sampling biases,

80 with research not always targeting the areas or species with the largest knowledge gaps (Di

81 Marco *et al.,* 2017). Indeed, research can be geographically biased not only at the country level,

82 but also towards specific regions, ecosystems, and land use categories (Velasco et al., 2015).

83 Resulting knowledge gaps can compromise the implementation of science-based conservation

84 interventions (Trimble and van Aarde, 2012), and biases might translate into policies, impacting

85 the achievement of biodiversity conservation targets (Velasco et al., 2015). It is therefore

86 important to understand and monitor these biases in research, in order to re-align research

87   priorities where needed (Di Marco et al., 2017; Donaldson et al., 2016). Given ongoing funding

88   shortfalls in conservation (Lindsey et al., 2018), it is especially important that limited resources

89   are directed toward where they are most needed (Trimble and van Aarde, 2012).

90   In the context of large carnivore population status assessment and monitoring, population density

91   is a commonly-employed and meaningful metric (Boitani and Powell, 2012). Although other

92   metrics of population status exist (e.g. occupancy – Strampelli et al., 2022b), population density

93   is increasingly recommended as the metric of choice to assess and monitor large carnivore

94   populations (Elliot and Gopalaswamy, 2016). In addition to estimating current status, estimating

95   densities also allows comparison over time and between sites, enabling researchers and managers

96   to understand how population status varies with biotic factors (Searle et al., 2021), anthropogenic

97   disturbances (Balme et al., 2010; Henschel et al., 2011), or land management strategies

98   (Swanepoel et al., 2015).

99   We carry out the first systematic review of all published, peer-review studies estimating

100 population density or abundance of large African carnivore populations over two decades (2000

101 – 2020). We determine research patterns and the geographical and taxonomic representativeness

102 of these studies, and identify biases and data gaps in population assessments and monitoring. We

103 also employ findings to discuss representativeness of different land use types in research efforts,

104 and the extent of involvement of authors from host countries. Finally, we use this information to

105 identify research priorities and opportunities for future large carnivore population assessments.

Materials & Methods

Literature review

We conducted a systematic review of published, peer-reviewed literature using Google Scholar

(last search: January 2021), compiling all studies where population density of one or more

African large carnivore species (lion, leopard, cheetah, African wild dog, spotted hyaena, striped

hyaena, brown hyaena) was either explicitly estimated, or derived from an empirically measured

parameter (e.g. home ranges). The review protocol was applied following the Preferred

Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al.,

2021; see Fig 1 for PRISMA flow diagram and Appendix S1 for PRISMA checklist). Literature

was searched by P.S. and S.N. by entering, in quotation marks, full scientific and vernacular

species names, as well as "density", "abundance", "population", "assessment", or "survey". Both

"hyaena" and "hyena" were used in the search.

Our intention was to review trends and biases in peer-reviewed literature over the past two

decades, and in doing so help identify priorities for assessments for the coming two decades. As

a result, only studies published between 1st January 2000 and 31st December 2020 were

considered. Due to the number of articles returned using Google Scholar searches, only the first

100 results for each search were considered. P.S. and S.N. screened the resulting records, and all

papers that did not include density or abundance estimation as an output were excluded (Fig. 1).

There were no disagreements on classifications.

Only estimates published in peer-reviewed literature were considered, to ensure data and

information quality (Suryawanshi et al., 2019). In addition, due to many unpublished reports not

being publicly available, studies published in the scientific literature are those most readily

128   available to most policy makers, conservation managers, and researchers, and therefore most

129   likely to influence international conservation policy and the disbursement of conservation

130   funding (Giam and Wilcove, 2012). Finally, the fact than many such reports are not publicly

131   available would have also led to any search for population assessment in grey literature being

132   incomplete, and to considerable study biases.

133   Although it was not necessary for population density to be the primary parameter of interest in

134   the study, studies were only included if the methodology employed to obtain density estimates

135   was described, thus providing the opportunity for this aspect of the study to be subjected to peer

136   review. Studies estimating population abundance were included only if the size of the sampled

137   area was explicitly defined and measured. Estimates reported in a peer-reviewed study from non-

138   peer reviewed sources (e.g. Weise et al., 2017), where the methodology employed was not

139   described (e.g. Balme et al., 2017), or where estimates for a wider area were obtained indirectly

140   by extrapolating from a smaller sampled area (e.g. Trinkel, 2009) were not included. We also did

141   not include density estimates from intensively managed populations (e.g. Buk et al., 2018), as the

142   exact number of individuals being known prior to the study precluded the type of 'exploratory'

143   surveys of interest in this review. This was only relevant to some populations of lion, cheetah,

144   and African wild dog in South Africa.

145   For each study that fitted the above criteria, we extracted information on: year of publication,

146   year(s) of data collection, authors' nationality (national of study country or foreigner, based on a

147   web search), study area, ecosystem, country, region, land use type (as described in the

148   publication; if multiple uses occurred – e.g. photographic tourism and trophy hunting – both

149   were listed), density estimate, and estimation method. Risk of bias was minimised by searching

150   for multiple possible terms in Google Scholar and by the clear-cut definitions of inclusion

151   employed.

152   Finally, we are aware of recent debates regarding the reliability of some large carnivore

153   population assessment methods (e.g. Braczkowski et al., 2020; Dröge et al., 2020), and of

154   common issues in large carnivore density estimation studies, such as that of under-sampling the

155   study area (Suryawanshi et al., 2019). However, given that our goal was to assess research effort,

156   we did not make distinctions based on methods employed, or on other features of the studies

157   themselves.

158   ***Analyses***

159   Findings of the literature review were employed to identify taxonomic trends in research effort,

160   including the total number of studies and the study density (studies per km^2 of geographical range)

161   per species. Geographic range maps and data for each species were obtained from the IUCN Red

162   List (https://www.iucnredlist.org/). Although we acknowledge some of these may be outdated or

163   imperfect, we reasoned this was the best way to remain consistent across species. We also

164   determined spatial patterns in research, through the total number of studies and the study density

165   per country and per region, both by species and overall. Finally, we investigated patterns in land

166   tenure of the areas where research was carried out, and the nationality (local national versus

167   foreigner) of the authors of the research.

168   We employed Generalised Linear Mixed Models (GLMMs) and Generalised Linear Models

169   (GLMs) to investigate taxonomic and spatial biases in large carnivore population assessments.

170   Models that combined species were fitted by Poisson GLMMs, with the number of studies coded

171   as the explanatory variable. Country and Species were included as random effects (random

172   intercepts) to control for multiple observations (i.e. data points for multiple species in each country,

173   and for multiple range countries for each species), and to investigate research biases (see below).

174   All models were validated by posterior predictive checks, dispersion parameters, and model

175   residuals (Appendix S5).

176   To first determine overall biases in research effort by species and countries, a model was built with

177   only Species and Country as random effects (Model 1). In this model, the random intercepts

178   represent relative differences in the number of surveys for that species or country; positive values

179   indicate a greater than average number of studies for that species or country, while negative values

180   indicate a lower than average number of studies, with the magnitude indicating the degree of

181   difference.

182   Species with larger geographical ranges could be expected to receive greater research attention by

183   chance. Therefore, to control for this, we then fit a model controlling for differences in species'

184   geographical range (Range) between countries, with Range modelled as a fixed effect and Country

185   and Species and random effects (Model 2). This allowed us to (a) test whether greater research

186   effort was directed towards species and countries with larger ranges; and (b) assess biases in

187   research, by country and by species, after controlling for differences in geographical range. For

188   this model, the random intercepts indicate whether the number of studies for a species or in a

189   country was more or less than expected according to the range of that species or in that country.

190   All analyses followed a Bayesian approach to parameter estimation using JAGS (Plummer, 2003)

191   in R (version 3.6.1; R Core Team, 2019) with the package *runjags* (Denwood, 2020). The fixed

192   explanatory variable ('range') was standardised to have a mean of 0 and standard deviation of 1,

193   to improve MCMC (Markov Chain Monte Carlo) convergence (Zuur et al., 2013). All models used

194   three MCMC chains, diffuse priors, and ran for enough iterations to produce an effective sample

195   size >10,000 (Kruschke and Liddell, 2018). MCMC chain convergence was confirmed with trace-

196   plots and the Gelman-Rubrin statistic. Variables (both fixed and random effects) were considered

197   to have a significant effect if they exhibited a credible non-zero effect (i.e. zero not contained

198   within the 95% highest density interval (HDI) of the posterior distribution).

199   In addition to the all-species GLMMs, GLMs were also built for each species to investigate

200   species-specific research biases. GLMs were used over GLMMs as – unlike the all-species models

201   – datasets for individual species did not have multiple observations per country, thus allowing their

202   applicability. Country biases were assessed using the model residuals: a positive residual signified

203   a country had more studies than expected, while a negative residual signified fewer. Residuals

204   considered credibly different from zero were those for which zero was not contained in the 95%

205   highest density interval (HDI).

206   GLMs were first fitted with a Poisson distribution (as we employed discrete count data) and

207   validated by posterior predictive checks, dispersion parameters, and model residuals. Poisson

208   distribution assumes that the mean and variance of the data are equal; if a Poisson model was not

209   suitable for the data, a more complex negative binomial model was used, validated by the same

210   methods employed for the GLMMs (Appendix S5). Through this method, leopard, spotted hyaena,

211   and cheetah data were fitted with Poisson GLMs with one outlier removed to reduce

212   overdispersion; lion data were fitted with a negative binomial GLM. African wild dog, striped

213   hyaena, and brown hyaena could not be modelled individually due to too few data points (range

214   countries) and/or insufficient variance (i.e. most range countries had zero studies).

215   **Results**

216   ***Literature review and research trends***

217   Our search of the published literature revealed 115 peer-reviewed articles (studies) which

218   estimated population density of one or more African large carnivore species. These provided a

219   total of 312 estimates of large carnivore population density, inclusive of all species (Fig. 2, 3).

220   Studies were predominantly carried out on protected land managed by the government (63%),

221   followed by private reserves (19%), land under community-based management (16%), and

222   unprotected areas (10%). Land tenure was unclear for 2% of studies. 83% of studies took place in

223   areas where non-consumptive (photographic) tourism occurred, 33% in an area with livestock

224   ranching, game ranching, and/or farming, 15% in an area with trophy hunting, and 3% in a logging

225   or mining concession. 71% of studies included a national of the study country as an author. For

226   studies outside of South Africa, however, only 59% of studies included a national of the study

227   country as an author. See Appendix S2 for a complete list of all studies and associated information,

228   and Appendix S3 for additional details on the data interpretation.

229   ***Taxonomic trends and biases***

230   The lion was the species with the greatest number of population density assessments in peer-

231   reviewed literature (55 studies which fitted the described criteria, leading to 90 estimates of

232   population density), followed by spotted hyaena (34 studies, 81 estimates), leopard (33 studies, 71

233   estimates), cheetah (19 studies, 21 estimates), brown hyaena (11 studies, 39 estimates), African

234   wild dog (6 studies, 7 estimates), and finally striped hyaena (3 studies, 3 estimates) (Fig. 3). Results

235   from the GLMM Model 1 (Fig. 4, Table S9) confirmed that more studies than average were

236   conducted on lion (which exhibited a significant positive bias) and on spotted hyaena, leopard,

237   brown hyaena and cheetah, and fewer than average on African wild dog and striped hyaena (with

238   the latter exhibiting a significant negative bias). Lion was also the species with the greatest study

239 density (studies per 100,000 km² of range), with this being an order of magnitude greater than for

240 all other species (Fig. 3).

241 After controlling for differences in geographical range (GLMM Model 2), there were still

242 significantly fewer studies than expected on striped hyaena; in fact, the species' very large

243 geographical range (Table S1) resulted in the negative bias for the species increasing (Table 1, Fig.

244 4). Lion still experienced a significant positive bias, while results suggest that the negative effect

245 for African wild dog and the positive effect for spotted hyaena were partly explained by their

246 restricted and large geographical ranges, respectively (Table S1; Fig. 4).

247 ***Geographical trends and biases***

248 *Regional*

249 Across all species, southern Africa was the region with the greatest number and density of large

250 carnivore population assessments, followed by eastern Africa (Table 2).

251 The greatest number of published lion population assessments came from eastern Africa, followed

252 by southern, central, and finally western Africa (see Table S1 for regional-level species-specific

253 insights). Nevertheless, western Africa exhibited the highest density of lion assessments, due to

254 the species' limited range in the region. Most leopard population assessments were carried out in

255 southern Africa, with more than twice the number of studies than in all other regions combined.

256 Cheetah population assessments also primarily took place in southern Africa, followed by eastern

257 (which exhibited the greatest study density) and northern Africa, with none in western or central

258 Africa. African wild dog assessments were relatively evenly spread across the continent. Most

259 spotted hyaena population estimates were from southern Africa (also exhibiting the greatest study

260 density), followed by eastern and central Africa; no studies took place in western or northern

261   Africa. All three of the published striped hyaena population assessments took place in eastern

262   Africa. Finally, brown hyaena assessments were only carried out in Southern Africa, the only

263   region where the species is present.

264   *Country*

265   South Africa was the country with the greatest total number of large carnivore population

266   assessments, followed by Tanzania, Kenya, and Botswana. Study density, instead, was highest in

267   Niger, followed by South Africa, Kenya, and Cameroon. Twenty-seven countries with at least one

268   large carnivore species (57%) had no published density estimation studies (Table 3). Results from

269   the GLMM Model 1 confirmed these results (Table S9). When controlling for range (GLMM

270   Model 2), South Africa then Kenya still exhibited the strongest bias, while Tanzania dropped to

271   fifth, with Cameroon and Botswana ranking higher (Table 1; Fig. 5). Chad, South Sudan,

272   Democratic Republic of Congo (DRC), and Angola ranked lowest, due to the combination of large

273   country range and a lack of studies (Table 3; Fig. 5).

274   Across all species, geographical range had a significant positive effect (GLMM Model 2; Table

275   1), indicating that having more species range in a country was associated with more studies. For

276   individual species (GLMs), geographical range had a significant positive effect on the number of

277   lion, leopard, and spotted hyaena population assessments within a country, but not on those of

278   cheetah (Table 4, Tables S10-S12).

279   For individual species, Tanzania was the country with the greatest number of lion assessments,

280   followed by Kenya and South Africa. Uganda was the country with the highest lion study density;

281   if we only consider countries with >40,000 km^2 of lion range, however, South Africa exhibited the

282   greatest study density, followed by Kenya, Zimbabwe, and Zambia. Central African Republic

283   (hereafter CAR), Ethiopia, Namibia, and Mozambique all exhibited large species range, but few

284   studies. Six countries (24%) had no published lion population assessments (Table S2). The GLM

285   results revealed that Kenya, South Africa, and Cameroon had significantly more lion population

286   assessments than would be expected based on country range, while CAR and South Sudan the

287   fewest (Table 4).

288   For leopard, South Africa was the country with the most assessments by a wide margin (almost

289   half of all studies). Only 28% of leopard range states had a published estimate, and the two with

290   the greatest leopard range in Africa, Angola and the DRC, had none (Table S3). When controlling

291   for geographical range in the GLM, South Africa was an outlier, exhibiting the largest positive

292   bias in studies, and Zimbabwe, Cameroon and Kenya also had significantly more assessments than

293   would be expected based on geographical range. Angola, DRC, and Ethiopia were the most

294   understudied (Table S10).

295   Botswana and Kenya were the countries with the most cheetah assessments, followed by Namibia

296   and Tanzania. 60% of cheetah range states had no published assessments, including some with

297   large tracts of range (Chad, Ethiopia; Table S4). Kenya, Botswana, and Tanzania were the

298   countries with the strongest positive bias after controlling for range in the GLM, while Algeria,

299   Chad, and Ethiopia those exhibiting the strongest negative research bias (Table S11). Peer-

300   reviewed African wild dog population assessments were only carried out in four countries: South

301   Africa, Kenya, Zimbabwe, and CAR. Study density was highest in South Africa. Overall, 78% of

302   range countries had no published African wild dog population assessments, including the five

303   countries with the largest geographical range (Table S5).

304   South Africa, Cameroon, Ethiopia, Kenya, and Namibia had the most spotted hyaena studies.

305   Cameroon had the highest study density, followed by South Africa and Congo. 24 range countries

306   (63%) had no studies (Table S6), including Angola and DRC, the countries with the first and third

307   greatest species range. Cameroon, South Africa, and Namibia exhibited the largest values of the

308   random intercepts when accounting for geographical range in the GLM, and Angola, DRC, and

309   Nigeria the smallest (Table S12). For striped hyaena, peer-reviewed assessments have only taken

310   place in Kenya, with 96% of range states having no published density estimates (Table S7). Finally,

311   South Africa then Botswana were the countries with the most brown hyaena population

312   assessments, and Botswana, Zimbabwe, and South Africa those with the highest study density.

313   Four range countries (50%) had no studies (Table S8).

Discussion

Taxonomic representativeness and biases

316   Over the past two decades, lion is the species that has received the greatest number of population

317   assessments, both overall (Fig. 2) and relative to species' geographical range (Table 1). It is likely

318   that the lion's highly charismatic nature (Macdonald et al., 2015), its role as a keystone and

319   flagship species (Bauer et al., 2015b; Leader-Williams and Dublin, 2000), and its ability to attract

320   conservation funding and generate revenue through tourism (Maciejewski and Kerley, 2014) all

321   play a role. In addition, a variety of methodologies have been employed to survey lion populations,

322   including some which cannot typically be applied to most other large carnivore species due to

323   behavioural differences (e.g. 'call-ins'; Braczkowski *et al.*, 2020). This likely also played a part in

324   the species receiving greater research attention.

325   The large number of studies on spotted hyaena, the second most studied species, are instead likely

326   partly driven by its vast distribution (as indicated by our findings; Fig. 4), and by the relatively

327   large number of methods used to survey the species (Davis et al., 2022). In addition, assessments

328   primarily targeting lions have often employed the data collected to also estimate spotted hyaena

329   density (e.g. Ferreira & Funston, 2016). Nevertheless, the fact that – due to the species' wide

330   distribution – study density was still relatively low (Fig. 3) suggests that considerable knowledge

331   gaps remain across its range, especially in western and central Africa.

332   Striped hyaena had the lowest number of population assessments, and the strongest negative

333   research bias (Table 1, Fig. 4). This is in line with previous suggestions that knowledge of the

334   species is particularly low (AbiSaid and Dloniak, 2015), and is likely due to a combination of

335   factors, including: populations often existing outside of formally protected areas (PAs; AbiSaid &

336   Dloniak, 2015); the species being more secretive and less well-known (Macdonald et al., 2015),

337   and thus less apt at raising conservation and tourism revenue (Di Minin et al., 2013; Okello et al.,

338   2008); and the fact that much of its range is in northern Africa, a region exhibiting low levels of

339   conservation research in general (Agha et al., 2018; Hickisch et al., 2019; Trimble and van Aarde,

340   2012). Finally, the fact that some easily implementable methods used to survey other species (e.g.

341   call-ins) cannot be reliably applied to striped hyaena (AbiSaid and Dloniak, 2015) is likely to also

342   have played a part.

343   The other species that exhibited a negative bias in research was the African wild dog (although

344   this effect was not significant; Table 1, Fig. 4). This is of particular concern due to the species

345   being the most threatened of the African large carnivores (Woodroffe and Sillero-Zubiri, 2020),

346   and supports suggestions that conservation research can be poorly aligned with conservation

347   priorities (Di Marco et al., 2017; Wilson et al., 2016). The observed paucity of estimates for

348   African wild dog is likely a result of the species being less well-known compared to the felids

349   (Macdonald et al., 2015), and a combination of ecological and methodological factors. African

350   wild dogs are social, low density species, with very large home ranges that often range outside of

351   PA boundaries (Creel and Creel, 2002); as a result, survey methods often employed for other

352   species (e.g. camera trapping combined with capture-recapture modelling; Strampelli *et al.*, 2022)

353   are challenging to apply to African wild dogs, while others (e.g. call-ins) are less suitable due to

354   behavioural characteristics. Indeed, although rapid assessment methods such as spoor counts have

355   occasionally been employed to survey populations (Henschel et al., 2020), approximately half of

356   published density estimates were obtained through resource-intensive long-term studies or citizen-

357   science approaches, highlighting the difficulty associated with surveying the species rapidly. In

358   addition, most African wild dog populations in South Africa are part of an intensively managed

359   metapopulation (Nicholson et al., 2020) where the exact number of individuals is known, and were

360   therefore not eligible for our review, even though the populations are actively monitored.

361   Other species experienced weaker effects. Leopard exhibited a slight positive bias in research,

362   while there was little evidence of cheetah experiencing strong biases in either direction. The

363   suitability of leopard to camera trap (Searle et al., 2021) and sign-based (Henschel et al., 2020)

364   methods has facilitated assessments, as has its wide range and charismatic nature (Maciejewski

365   and Kerley, 2014). On the other hand, although cheetahs are highly charismatic (Di Minin et al.,

366   2013; Macdonald et al., 2015), listed as vulnerable to extinction (Durant et al., 2015), and have

367   high potential to generate conservation revenue through tourism (Maciejewski and Kerley, 2014;

368   Okello et al., 2008), a lack of rapid survey techniques for the species (Strampelli et al., 2021) likely

369   played a role in survey efforts not being greater. Additionally, the fact that – as for African wild

370   dog – numerous populations in South Africa inhabit small, intensively managed reserves (Buk et

371   al., 2018) also likely played a part in the estimates considered being relatively few.

372   For all species except cheetah, greater geographical range in a country was found to correspond to

373   greater research effort in that country (Table 4, Tables S10-12). Nevertheless, our findings suggest

374   that a range of additional factors, including the species' ecology, charisma, ability to generate

375   conservation funding and tourism revenues, and applicability of different survey methods all play

376   a role in driving the extent of population assessments for a species.

377   ***Regional trends and biases***

378   Greater research effort in southern Africa (Table 2) is likely a result of greater conservation

379   investments in the region (Brockington and Scholfield, 2010; Wilson et al., 2016) and the better

380   socio-economic status of some countries (UNDP, 2020). For most species, eastern Africa was the

381   second most studied region; this is likely due to the region still harbouring numerous important

382   large carnivore populations (Table S1), as well as the long history of conservation investments and

383   research in some countries (e.g. Kenya, Tanzania; Brockington & Scholfield, 2010).

384   Low research effort in northern Africa is likely due to most large carnivore populations in the

385   region existing at low density and outside of PAs (Belbachir et al., 2015), to conservation research

386   investments being comparatively low, and to the political instability of some countries (Di Marco

387   et al., 2017; Wilson et al., 2016). Similarly, the low level of research in northern, western, and

388   central Africa for most species (Table S1) mirrors the region's under-representation across wider

389   conservation research (Hickisch et al., 2019; Trimble and van Aarde, 2012; Wilson et al., 2016).

390   For central Africa, this negative bias is likely primarily a consequence of high volatility and low

391   conservation investments in the region (Brockington and Scholfield, 2010; FFP, 2020). In western

392   Africa, the fact that conservation investments and wildlife-oriented tourism have historically been

393   lower than in southern and eastern Africa (Brockington and Scholfield, 2010; UNWTO, 2018) has

394   likely had an impact on research effort.

395   Our findings largely agree with suggestions of biases towards carnivore research and conservation

396   activities in eastern and southern Africa (Ray et al., 2005). Nevertheless, when accounting for

397   greater geographical range in these region, the density of population assessments was actually

398   lower than in central and western Africa for a number of species (Table S1). In addition, for several

399   species, many assessments in eastern Africa are from a small number of populations; for example,

400   approximately half (48%) of lion and 75% of cheetah assessments in the region were from a single

401   population, in the Serengeti-Mara (Appendix S2), even though this comprises only ~7% of lion's

402   and ~8% of cheetah's eastern African range. Without studies from the Serengeti-Mara, eastern

403   Africa would exhibit the lowest lion study density of any range region. Our findings therefore

404   suggest that after accounting for differences in geographical range and the repeated sampling of a

405   few populations, the observed biases in population assessments towards certain regions are less

406   clear-cut than they may initially appear, and that understudied populations remain even in the

407   regions receiving the most research attention.

408   ***Country trends and biases***

409   As lack of research can impede biodiversity conservation (Di Marco et al., 2017; Pullin et al.,

410   2004), the fact that 57% of African countries with large carnivore range did not have a single

411   published, peer-reviewed population assessment is of concern. When accounting for differences

412   in geographical range, Angola, South Sudan, DRC, and Chad exhibited the strongest negative bias

413   in research (Table 1), likely primarily as a consequence of years of political unrest and insecurity

414   in these countries (FFP, 2020).

415   South Africa showed the strongest positive bias in published research (Table 1), with the greatest

416   number of assessments for several species (Tables S2-S8). Conservation investments are

417   particularly high in South Africa (Brockington and Scholfield, 2010), likely explaining this bias.

418 Although Tanzania was the country with the second highest number of assessments, accounting

419 for geographical range caused the country to exhibit only the fifth strongest positive bias (Table

420 1), indicating that part of this effect is due to the country being home to considerable large

421 carnivore range. Furthermore, 60% of all published lion population assessments in the country

422 were from a single ecosystem (Serengeti), comprising only 8% of lion country range. A similar

423 bias was also observed in Kenya, with 45% of lion studies being from the Mara complex, even

424 though this accounted for only ~3% of national lion range. These biases towards a small number

425 of well-studied populations suggest that the total number of studies may not be a representative

426 indicator of how well a country's large carnivore populations have been studied.

427 Overall, our results suggest that the extent of published biological research in a country is

428 dependent on a range of factors, including socio-economic status, research history and interests of

429 individuals and organisations, priorities of funding agencies and governments, in-country support

430 and capacity, and language barriers to publication (Griffiths and Dos Santos, 2012; Trimble and

431 van Aarde, 2012).

432 ***Opportunities and recommendations***

433 Reducing the identified geographical and taxonomic biases in population assessments would help

434 ensure that all species and areas of conservation importance have an adequate knowledge base

435 available, improving their conservation outlook (Wilson et al., 2016). We argue that addressing

436 the identified geographical biases (by region, countries, and land use types) should be the most

437 pressing priority: while a focus towards certain species, such as lion, may indirectly lead to

438 conservation benefits for other species (e.g. by identifying areas requiring additional conservation

439 investments), research from well-studied areas is unlikely to be able to help inform conservation

440 decisions in poorly-studied regions (Di Marco et al., 2017). Thus, much like for the wider

441   conservation research field (Trimble and van Aarde, 2012), geographical biases in research and

442   assessments are more immediate hurdles for science-based conservation management of African

443   large carnivores. As a result, northern, western, and central Africa should be considered priority

444   regions for future research. Increased attention should in particular be given to the twenty-six

445   countries which currently lack any published estimates (Table 3), especially Angola, DRC, South

446   Sudan, and Chad, given their considerable large carnivore country ranges and their potential

447   importance for the conservation of these species (Dickman et al., 2015). Within southern and

448   eastern Africa, we encourage prioritising additional research outside of South Africa and the

449   Serengeti-Mara ecosystem, respectively, to complement the efforts there.

450   Shortfalls in conservation research in countries with high levels of biodiversity but low income

451   can be due to a lack of trained and/or funded biologists (Gaston, 2000), research infrastructure

452   (Wilson et al., 2016), or dedicated finances (Githiru et al., 2015). As a result, building capacity of

453   researchers and practitioners in large carnivore survey and monitoring techniques in under-

454   represented areas should be a priority. The fact that only 59% of studies outside of South Africa

455   included a co-author from the study country reinforces suggestions that research in developing

456   countries is disproportionately led by scientists from more developed areas (Stocks et al., 2008),

457   and shows there is considerable need for such capacity building efforts. For these reasons, we

458   recommend that both donors and foreign researchers maximise the involvement of local scientists,

459   students, and practitioners in future assessments, including through capacity building initiatives

460   such as the provision of training, funding, and equipment.

461   Conservation donors and funders should encourage efforts in understudied regions, as well as for

462   understudied species, to ensure that conservation research occurs where it is most needed (Di

463   Marco et al., 2017; Wilson et al., 2016). This is especially important the case given widespread

464   funding shortfalls in conservation (Lindsey et al., 2018). At the same time, we also urge funders

465   and practitioners to recognise the importance of scale dependency, as even within more studied

466   countries gaps remain: in Tanzania, the country with the greatest lion range and the most lion

467   studies, most populations are nevertheless yet to be assessed. We therefore emphasize the

468   importance of decision and investment processes being multi-scale, and of appreciating the

469   intricacies of the identified biases.

470   On a species level, we echo calls for further population assessments of striped hyaena (AbiSaid

471   and Dloniak, 2015). We also strongly recommend prioritising further population assessments of

472   African wild dog, particularly due to the species' classification as 'Endangered' (Woodroffe and

473   Sillero-Zubiri, 2020). Such efforts are especially required in countries that have been identified as

474   critical for the species, but where no recent assessments have been carried out (e.g. Botswana and

475   Tanzania; Kuiper et al., 2018). As the lack of well-established methods to rapidly survey African

476   wild dog populations is a key reason for these knowledge gaps (Woodroffe and Sillero-Zubiri,

477   2020), longer-term intensive monitoring studies such as those carried out prior to this review's

478   considered period (e.g. Creel & Creel, 1996), alongside further development of novel, cost-

479   effective methodologies (e.g. citizen-science techniques; Marnewick et al., 2014), are strongly

480   recommended. The possibility of monitoring populations through alternative status parameters,

481   such as species' occupancy (Henschel et al., 2020), should also be explored.

482   Our findings also highlight the urgent need for additional cheetah population assessments,

483   particularly in northern, western, and central Africa. Due to their large country ranges, studies in

484   Chad and Ethiopia should especially be considered a priority. As in the case of African wild dog,

485   we also recommend further development and standardisation of cheetah population monitoring

486   techniques, including the exploration of citizen-science based approaches (Marnewick et al., 2014;

487   Weise et al., 2017).

488   For leopard, surveys are particularly recommended in the 72% of range states without published

489   estimates, particularly those with large geographical range (Angola, DRC, Ethiopia, and South

490   Sudan; Table S3). Although considered a highly adaptable species, leopard populations are

491   increasingly under threat (Stein et al., 2020). It is therefore important that research and monitoring

492   is carried out across the species' range, rather than in localised 'hubs', as is currently the case

493   (South Africa; Table S3).

494   For spotted hyaena, future efforts should prioritise populations in northern and western Africa, as

495   no assessments are available from these regions, as well as in countries with extensive range but

496   no surveys (Angola, DRC, Nigeria, Somalia, and South Sudan). For brown hyaena, we recommend

497   the prioritisation of assessments across different habitats and land-use types (Kent and Hill, 2013),

498   and in countries where the species is yet to be surveyed (Angola, Mozambique, Eswatini; Table

499   S8).

500   Study density for lion was lowest in central Africa, which should therefore be considered a priority

501   region for further assessments. Nevertheless, considerable opportunity for further work exists in

502   most range countries; even in Tanzania and Kenya, the two with the greatest number of

503   assessments, most populations have not been empirically assessed. Overall, the fact that even for

504   lion, the species with the strongest positive bias in research, considerable gaps still exist highlights

505   the extent to which African large carnivore populations are presently understudied and under-

506   monitored.

507   Finally, efforts should be made to address the observed sampling bias towards photographic

508   tourism areas, and against trophy hunting areas. Trophy hunting areas in Africa cover a greater

509   area than National Parks (Lindsey et al., 2007), and, given that accurate estimates of population

510   size are crucial to ensure the sustainability of trophy hunting (Mweetwa et al., 2018), we

511   recommend that future efforts attempt to bridge this gap. Similarly, although working on public

512   and/or unprotected land can be logistically challenging (Agha et al., 2018), efforts should also be

513   made to address the negative sampling bias associated with these areas, as our findings support the

514   global pattern of biodiversity monitoring largely taking place within PA networks (Martin et al.,

515   2012). The fact that some species still heavily occupy areas outside PAs (e.g. spotted hyaena,

516   Bohm & Höner, 2015; cheetah, Weise et al., 2017), and that non-protected areas encompass the

517   majority of wildlife habitat across the continent (Agha et al., 2018), highlights the need for future

518   efforts to include boundary and non-protected areas.

519   **Conclusions**

520   We carried out the first review of peer-reviewed African large carnivore population assessments,

521   focusing on the last two decades, and empirically tested for geographical and taxonomic biases

522   in effort. We found research biases towards lion and against striped hyaena, and to a lesser extent

523   African wild dog. Assessments were biased towards southern and eastern Africa, while northern,

524   western, and central Africa were generally under-studied. Non-protected and trophy hunting

525   areas were under-sampled compared to photographic tourism areas. Significant opportunities

526   exist for greater inclusion of host country nationals in such studies, and we recommend increased

527   capacity building and provision of funding for researchers from range countries. Overall, we

528   recommend the biases we have identified are employed by researchers, practitioners, and

529   policymakers to address knowledge gaps and help inform future research and monitoring efforts.

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Figure 1

PRISMA flow diagram

PRISMA flow diagram for methodology for syntethic review of African large carnivore assessments (2000-2020).

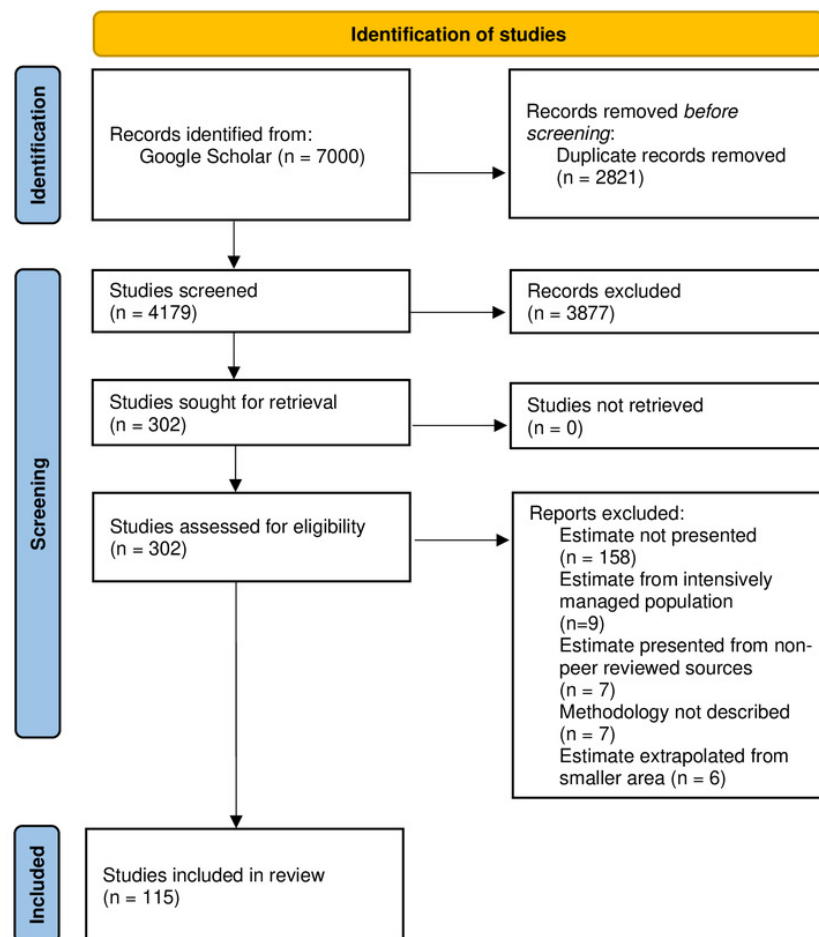



Figure 2

Location of peer-reviewed African large carnivore studies (2000-2020)

Location of peer-reviewed African large carnivore population assessment studies (2000 3 2020). Red crosses show estimates of population density, except in the case of brown hyaena, where blue crosses are used. When a study estimated multiple population densities, these are shown as separate points. Grey areas represent current geographical ranges (IUCN, 2020), except in the case of brown hyaena, where a dotted pattern is used. Diûerent symbols were used for brown hyaena in order to facilitate presentation of the data.

Lion
Panthera leo

Leopard
Panthera pardus

Cheetah
Acinonyx jubatus

African wild dog
Lycaon pictus

Spotted hyaena
Crocuta crocuta

Striped hyaena
Hyaena hyaena

Brown hyaena
Parahyaena brunnea

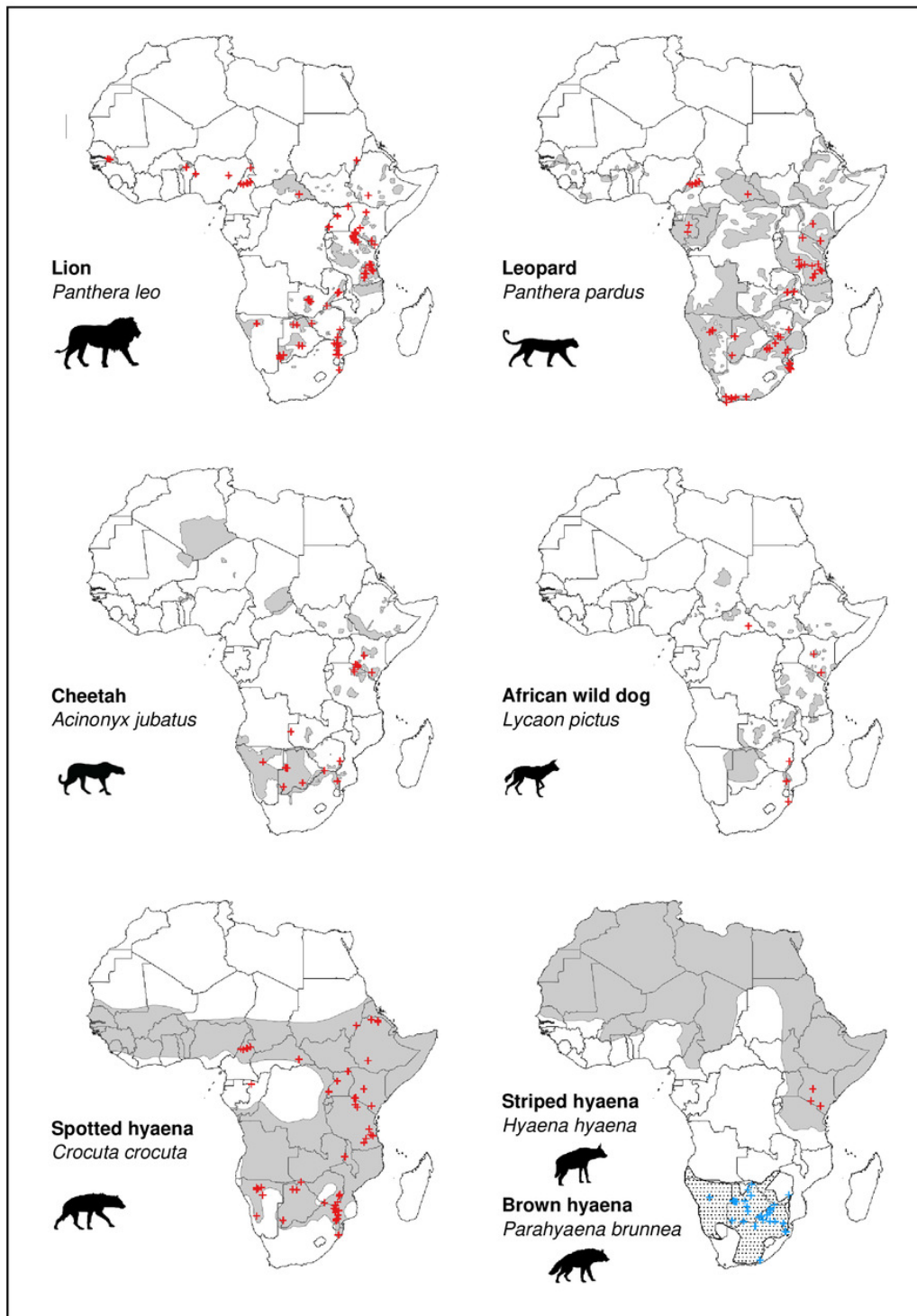



Figure 3

Summary of peer-reviewed African large carnivore density assessments, by species

Number of peer-reviewed population density assessments (studies), number of individual

population density estimates, and density of peer-reviewed studies (studies per 100,000 km^2

of geographical range) for African large carnivores (2000 – 2020). Species are presented in

decreasing order by number of studies.

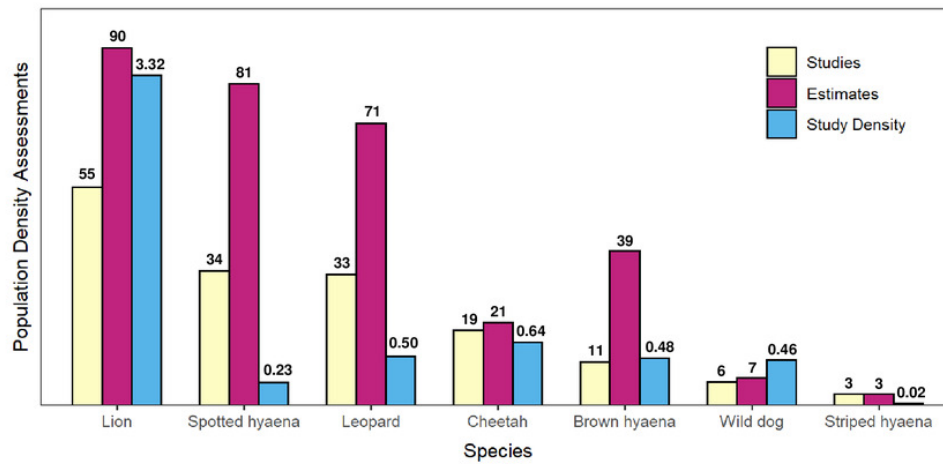



Figure 4

Random intercept values for species from the Poisson GLMMs

Random intercept values for species from the Poisson GLMM without explanatory variables (Model 1, Table S9) and for that accounting for geographical range (Model 2, Table 1). In both cases, values for lion and striped hyaena were credibly different from zero (i.e. zero not contained within the 95% HDI of the posterior distribution; shown in blue), with this being strongest when accounting for geographical range of species. The moderate negative effect for African wild dog and positive effect for spotted hyaena, on the other hand, were partly explained by their restricted and very large geographical ranges, respectively.

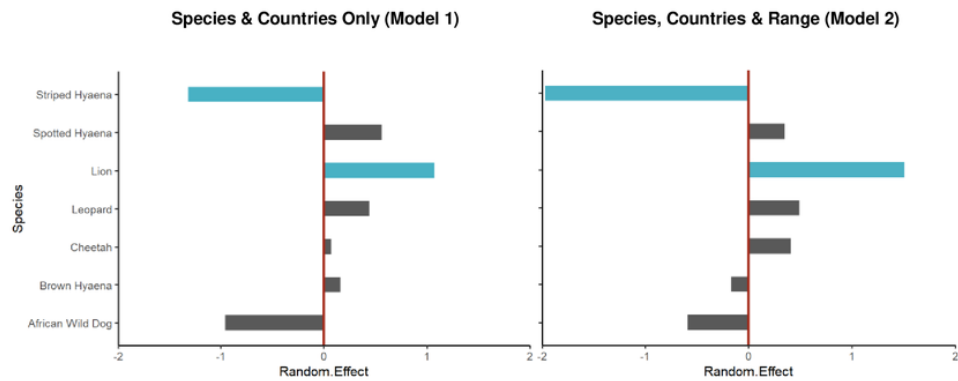
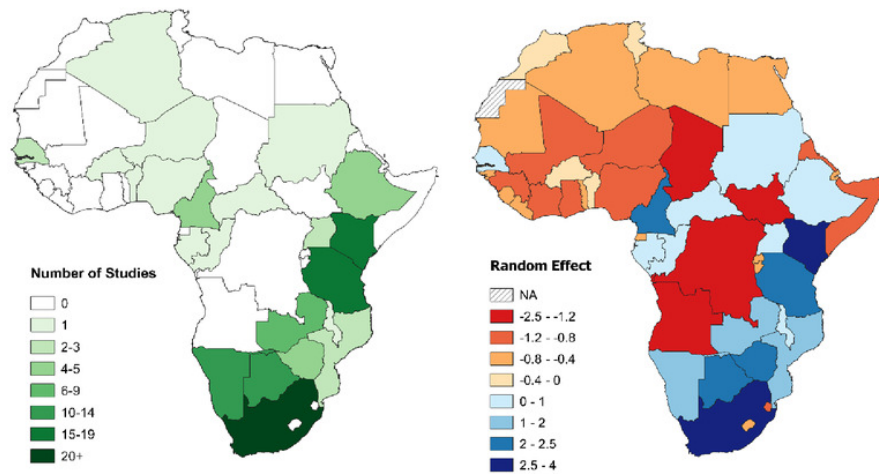



Figure 5

Number of large carnivore population assessment studies in Africa and random effects
for individual countries

Left: Number of large carnivore population assessment studies in Africa, by country. Right:
Random effects for individual countries from the Poisson GLMM investigating biases in large
carnivore population assessments in Africa, accounting for differences in geographical range
between countries (Model 2). A positive value (blue) indicates more population assessments
than expected based on large carnivore geographical range within the country, while a
negative value (red) fewer (all species combined). See Table 1 for country specific values. For
all figures in this study, country boundaries are based on the definitions of the African Union (
https://web.archive.org/web/20130927110741/http://www.afrimap.org/english/images/report/
AfriMAP-AU-Guide-EN.pdf

Results of the Poisson GLMM investigating biases in large carnivore population assessments in Africa, accounting for differences in geographical range between countries (Model 2).

Results of the Poisson GLMM investigating biases in large carnivore population assessments in Africa, accounting for differences in geographical range between countries (Model 2). Species and countries are modelled as random effects. For species, a positive value indicates more assessment than expected given their geographical range, while a negative fewer. For countries, a positive value indicates more assessments than expected based on large carnivore geographical range within that country, while a negative fewer. Values credibly different from zero (i.e. 95% highest density interval (HDI) of the posterior distribution does not contain zero) are highlighted in bold for species and range.

Table 1. Results of the Poisson GLMM investigating biases in large carnivore population assessments in Africa, accounting for differences in geographical range between countries (Model 2). Species and countries are modelled as random effects. For species, a positive value indicates more assessment than expected given their geographical range, while a negative fewer. For countries, a positive value indicates more assessments than expected based on large carnivore geographical range within that country, while a negative fewer. Values credibly different from zero (i.e. 95% highest density interval (HDI) of the posterior distribution does not contain zero) are highlighted in bold for species and range.

Name	Mean	HDI low	HDI high	SD
Intercept	-2.07	-3.60	-0.65	0.75
Range *	**0.60**	**0.26**	**0.93**	**0.17**
Country Random Effect Variance	1.70	1.07	2.46	0.37
Species Random Effect Variance	1.46	0.52	2.78	0.69
Brown Hyaena	-0.17	-1.53	1.20	0.69
Cheetah	0.41	-0.91	1.75	0.67
Leopard	0.49	-0.76	1.80	0.65
Lion *	**1.51**	**0.29**	**2.88**	**0.66**
Spotted Hyaena	0.35	-0.93	1.65	0.65
Striped Hyaena †	**-1.97**	**-3.82**	**-0.39**	**0.89**
African Wild Dog	-0.59	-2.00	0.82	0.71
South Africa *	3.13	2.24	4.08	0.48
Kenya *	2.91	2.02	3.87	0.48
Cameroon *	2.47	1.45	3.56	0.54
Botswana *	2.38	1.43	3.38	0.50
Tanzania *	2.19	1.21	3.24	0.52
Zimbabwe *	2.10	1.05	3.20	0.55
Namibia *	1.68	0.62	2.78	0.55
Zambia *	1.48	0.36	2.64	0.58
Mozambique	1.04	-0.18	2.28	0.63
Uganda	0.96	-0.48	2.37	0.73
CAR	0.92	-0.40	2.20	0.66
Ethiopia	0.86	-0.38	2.12	0.63
Malawi	0.73	-0.95	2.31	0.83
Senegal	0.61	-1.04	2.18	0.82
Gabon	0.50	-1.59	2.48	1.04
Congo	0.44	-1.61	2.41	1.03
Nigeria	0.41	-1.71	2.34	1.03
Sudan	0.27	-1.34	1.79	0.79
Tunisia †	-0.16	-3.42	3.03	1.64
Benin †	-0.17	-2.04	1.68	0.95
Burkina Faso †	-0.19	-2.09	1.63	0.95
Morocco †	-0.36	-3.40	2.64	1.55
Algeria †	-0.44	-2.49	1.50	1.02
The Gambia †	-0.52	-3.48	2.29	1.48
Lesotho †	-0.55	-3.48	2.23	1.47
Equatorial Guinea †	-0.56	-3.37	2.28	1.46
Djibouti †	-0.58	-3.50	2.10	1.44

Egypt [†]	-0.70	-3.57	1.92	1.42
Mauritania [†]	-0.70	-3.51	1.96	1.42
Libya [†]	-0.74	-3.61	2.00	1.44
Rwanda [†]	-0.76	-3.56	1.86	1.40
Burundi [†]	-0.76	-3.54	1.85	1.40
Sierra Leone [†]	-0.77	-3.62	1.77	1.39
Guinea-Bissau [†]	-0.77	-3.56	1.82	1.39
Liberia [†]	-0.77	-3.59	1.81	1.39
Togo [†]	-0.80	-3.53	1.83	1.39
Eritrea [†]	-0.82	-3.54	1.78	1.38
Ghana [†]	-0.82	-3.57	1.72	1.37
Guinea [†]	-0.84	-3.62	1.65	1.37
Cote d'Ivoire [†]	-0.85	-3.58	1.68	1.37
Eswatini [†]	-0.86	-3.65	1.67	1.37
Somalia [†]	-1.04	-3.67	1.38	1.31
Nigeria [†]	-1.13	-3.69	1.26	1.29
Mali [†]	-1.14	-3.74	1.26	1.30
Niger [†]	-1.14	-3.79	1.20	1.29
Chad [†]	-1.42	-3.91	0.85	1.23
South Sudan [†]	-1.42	-3.91	0.84	1.24
DRC [†]	-1.57	-4.05	0.59	1.21
Angola [†]	-1.72	-4.09	0.47	1.18

Legend: HDI = Highest Density Interval; SD = standard deviation; Range = country range, based on IUCN Red List polygons (IUCN, 2020); * = value suggests significant positive effect; [†] = value suggests significant negative effect.

Regional geographical trends in large carnivore research in Africa (2000 – 2020), all species combined

Regional geographical trends in large carnivore research in Africa (2000 – 2020), all species combined. All figures were obtained by combining estimates of geographical range, studies/estimates, and density of studies/estimates for all large carnivore species. See Table S1 for species-specific insights.

Table 2. Regional geographical trends in large carnivore research in Africa (2000 – 2020), all species combined. All figures were obtained by combining estimates of geographical range, studies/estimates, and density of studies/estimates for all large carnivore species. See Table S1 for species-specific insights.

Region	Geographical Range (km²)*	Studies	Density Estimates	Studies / 100,000 km²	Estimates / 100,000 km²
Southern	12,114,919	62	176	0.51	1.45
Eastern	12,587,456	38	86	0.30	0.68
Central	6,116,580	7	40	0.11	0.65
Western	4,832,540	5	8	0.10	0.17
Northern	8,145,160	1	1	0.01	0.01

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

Large carnivore population assessments in Africa (2000-2020) by country, all species combined.

Large carnivore population assessments in Africa (2000-2020) by country, all species combined. Figures were obtained by combining estimates of geographical range, studies/estimates, and density of studies/estimates for all large carnivore species. Refer to Tables S2 – 8 for species-specific insights.

Table 3. Large carnivore population assessments in Africa (2000-2020) by country, all species combined. Figures were obtained by combining estimates of geographical range, studies/estimates, and density of studies/estimates for all large carnivore species. Refer to Tables S2 – 8 for species-specific insights.

Country	Studies	Estimates	Geographical Range (km²) *	Studies / 100,000 km²	Estimates / 100,000 km²
South Africa	27	88	1,601,900	1.69	5.49
Tanzania	16	41	2,871,700	0.56	1.43
Kenya	15	31	1,735,300	0.86	1.79
Botswana	11	38	2,469,150	0.45	1.54
Namibia	10	16	2,388,600	0.42	0.67
Zambia	7	12	1,305,900	0.54	0.92
Cameroon	5	29	600,740	0.83	4.83
Zimbabwe	4	13	752,800	0.53	1.73
Ethiopia	4	5	2,884,486	0.14	0.17
Mozambique	3	4	1,413,300	0.21	0.28
Uganda	2	7	468,900	0.43	1.49
Senegal	2	2	349,800	0.57	0.57
CAR	1	10	1,147,040	0.09	0.87
Malawi	1	6	135,600	0.73	4.42
Gabon	1	3	255,600	0.39	1.17
Nigeria	1	2	1,012,000	0.10	0.20
Sudan	1	2	1,729,400	0.06	0.12
Niger	1	1	17,190	5.82	5.82
Benin	1	1	300,400	0.33	0.33
Congo	1	1	386,000	0.26	0.26
Burkina Faso	1	1	572,550	0.17	0.17
Algeria	1	1	3,089,900	0.03	0.03
Angola	0	0	2,009,200	0.00	0.00
Burundi	0	0	28,700	0.00	0.00
Chad	0	0	1,940,300	0.00	0.00
Cote d'Ivoire	0	0	273,400	0.00	0.00
Djibouti	0	0	24,800	0.00	0.00
DRC	0	0	1,751,000	0.00	0.00
Egypt	0	0	1,015,800	0.00	0.00
Equatorial Guinea	0	0	12,800	0.00	0.00
Eritrea	0	0	257,798	0.00	0.00
Eswatini	0	0	38,369	0.00	0.00
Ghana	0	0	209,100	0.00	0.00
Guinea	0	0	277,100	0.00	0.00
Guinea-Bissau	0	0	43,000	0.00	0.00
Lesotho	0	0	100	0.00	0.00
Liberia	0	0	41,200	0.00	0.00
Libya	0	0	1,758,000	0.00	0.00
Mali	0	0	1,602,600	0.00	0.00
Mauritania	0	0	1,140,960	0.00	0.00

Morocco	0	0	976,900	0.00	0.00
Rwanda	0	0	28,500	0.00	0.00
Sierra Leone	0	0	62,700	0.00	0.00
Somalia	0	0	1,314,700	0.00	0.00
South Sudan	0	0	1,271,872	0.00	0.00
The Gambia	0	0	11,300	0.00	0.00
Togo	0	0	54,600	0.00	0.00
Tunisia	0	0	163,600	0.00	0.00

* Based on IUCN Red List geographical range polygons (IUCN, 2020)

Results of the models investigating biases in lion population assessments in Africa, accounting for geographical range (Negative Binomial GLM).

Results of the models investigating biases in lion population assessments in Africa, accounting for geographical range (Negative Binomial GLM). For residuals of individual countries, a positive value indicates more assessments than expected after controlling for the relevant variables, a negative value fewer. Significant residual values (defined as zero not contained within the 95% highest density interval (HDI) of the posterior distribution) are highlighted. Names of fixed effects and of countries are in bold if the variable exhibits a significant (i.e. credible non-zero) effect. Similar results for other species are presented in Appendix S4.

Table 4. Results of the models investigating biases in lion population assessments in Africa, accounting for geographical range (Negative Binomial GLM). For residuals of individual countries, a positive value indicates more assessments than expected after controlling for the relevant variables, a negative value fewer. Significant residual values (defined as zero not contained within the 95% highest density interval (HDI) of the posterior distribution) are highlighted. Names of fixed effects and of countries are in bold if the variable exhibits a significant (i.e. credible non-zero) effect. Similar results for other species are presented in Appendix S4.

Name	Mean	HDI low	HDI high
(Intercept)	0.73	0.29	1.17
Range *	**0.51**	**0.08**	**0.95**
Kenya *	**3.46**	**1.59**	**5.36**
South Africa *	**2.35**	**0.94**	**3.73**
Cameroon *	**2.05**	**0.78**	**3.36**
Zimbabwe	0.66	-0.01	1.34
Zambia	0.62	-0.08	1.33
Uganda	0.36	-0.25	0.98
Botswana	0.35	-0.50	1.21
Tanzania	0.28	-1.09	2.12
Nigeria	-0.29	-0.67	0.10
Sudan	-0.3	-0.67	0.10
Burkina Faso	-0.31	-0.68	0.08
Benin	-0.31	-0.68	0.07
Senegal	-0.33	-0.69	0.04
Mozambique †	**-0.52**	**-0.96**	**-0.08**
Ethiopia †	**-0.63**	**-0.95**	**-0.31**
Namibia †	**-0.68**	**-1.02**	**-0.35**
Niger †	**-0.91**	**-1.21**	**-0.63**
Chad †	**-0.91**	**-1.21**	**-0.62**
Malawi †	**-0.92**	**-1.22**	**-0.63**
Angola †	**-0.92**	**-1.23**	**-0.63**
DRC †	**-0.92**	**-1.23**	**-0.64**
South Sudan †	**-0.93**	**-1.24**	**-0.64**
CAR †	**-0.99**	**-1.57**	**-0.49**