1 **Spatial distribution and research trend of illegal activities and the factors associated**
2 **with wild mammal population declines in protected areas**

3 Short title: Global review of the impact of poaching on wildlife in protected areas

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31

32 **Abstract**

33 Illegal activities are a persistent problem in many protected areas, but an overview of the
34 extent of this problem and its impact is lacking. We review 35 years (1980-1914) of
35 research across the globe to examine the spatial distribution of research and socio-
36 ecological factors influencing population decline within protected areas under illegal
37 activities pressure. From 92 papers reporting 1048 species/site combinations, more than
38 350 species comprising mammals, reptiles, birds, fishes and molluscs were reported to have
39 been extracted illegally from 146 protected areas across four continents. Research in illegal
40 activities has increased substantially during the review period but also shows strong
41 taxonomic and geographic biases towards large wild mammals and African continent
42 respectively, suggesting persistent poaching pressures on wild mammals in African
43 protected areas. Population declines were most frequent i) where there was commercial
44 poaching as opposed to subsistence poaching alone, ii) in countries with a low human
45 development index particularly in strict protected areas and iii) for species with a body
46 mass over 100 kg. Habitat loss associated with greater land use change had an additional
47 significant impact on population decline, particularly in the less-strict categories (IUCN III-
48 VI) of protected area across the continents. Overall, these findings provide evidence that
49 illegal activities are most likely to cause species declines of large-bodied animals in
50 protected areas in resource-poor countries regardless of protected area conservation status
51 (i.e. IUCN category). Given the mounting pressures of illegal activities, additional
52 conservation effort such as improving anti-poaching strategies and conservation resources
53 in terms of improving funding and personnel directed at this problem is a growing priority.

54

55 **Keywords:** human development index, illegal harvest, land use change index, megafauna,
56 population decline, protected areas

57

58 **Introduction**

59 Improving the spatial coverage of protected area (PA) network is increasingly viewed as a
60 global biodiversity conservation priority (1, 2). The global land area with legal protection
61 for conservation has increased from 3.5% in 1985 (3) to 13% recently (4) and looks set to
62 increase further as countries aim to fulfil the Aichi target of protecting 17% of terrestrial
63 land by 2020 (5). Despite this increase and the investment made in protected areas (6),
64 biodiversity loss is perceived to be continuing even in PAs. For example, Craigie, Baillie
65 (7) reported continent-wide population declines of large mammals across several of
66 Africa's protected areas. To allocate conservation resources efficiently, it is important to
67 understand the scale and trends of illegal activities. Most studies, e.g. Mitchell (8), Wright,
68 Zeballos (9), Leader-Williams, Albon (10) have focused on a single threat, on a single
69 protected area type or region, and/or over short time periods. These provide crucial PA-
70 specific data, but information on illegal activities and their impact at broader spatial and
71 temporal scales is sparse, making tackling illegal activities difficult. Here we review the
72 site-specific literature to assess the global and regional patterns and impacts of illegal
73 activities on species in protected areas and to provide information on the factors associated
74 with population decline that may help improve the conservation of existing protected areas.

75 Anthropogenic threats reported from within PAs include hunting, logging, settlement,
76 cultivation, livestock grazing etc. Each can reduce the ability of PAs to preserve
77 biodiversity effectively (11). Moreover, the ability of PAs to protect species can be

78 influenced by factors beyond their boundaries. For example, human-animal conflict has
 79 caused widespread mortality of carnivore species at and outside reserve borders,
 80 jeopardizing the persistence of populations inside protected areas, particularly for species
 81 with large home ranges that encompass both protected and unprotected land (12). At a
 82 larger scale, poaching of migratory species during periods when they are outside PAs has
 83 been reported as among the major threats imperiling the long-term conservation of species
 84 such as saiga (*Saiga tatarica*) and wildebeest (*Connochaetes taurinus*) antelopes, in Asia
 85 and East Africa respectively(13, 14). The ability of populations to sustain and recover from
 86 illegal activities within and surrounding PAs will depend on the type and level of activity,
 87 combined with the biological characteristics of the species affected by those activities. For
 88 example, selective poaching of males has been associated with the reproductive collapse
 89 and population decline of saiga (13), and species with low rates of reproduction and growth
 90 may be particularly prone to population decline and extinction (15).

91 While the studies above provide useful accounts of the threats facing PAs, relatively few of
 92 them quantify the relative contribution of individual threats to the overall pattern of
 93 population change and decline in PAs (16). Such an assessment is required to identify
 94 strategies to improve PA performance, such as where to target additional resources and
 95 which actions are most effective at enforcing existing regulations (17). Here, we review
 96 research published over 35 years (1980-1914) on illegal activities in PAs to understand the
 97 global and regional patterns and to assess their impacts on species in protected areas. We
 98 evaluate what factors determine the likelihood that illegal activities lead to the decline in
 99 the populations of targeted animals. In particular, we assess whether the different legal
 100 status in different PAs affects their ability to prevent population declines, and whether
 101 attributes of the species (i.e. body mass) and socio-economic context of a country (i.e.

human development and agricultural land use change statuses) account for differences in PA success. Finally, we draw on these results to propose recommendations for reducing impacts of illegal activities in protected areas.

Materials and Methods

Data collation

We searched Web of Science, Science Direct, Google Scholar and Scopus for all papers since 1950 using the search terms: illegal activit*AND protected area OR region name (e.g. Europe, Asia, North/South America, Africa and Australia, New Zealand) OR reserve OR biodiversity outcome. Further search was performed incorporating poach / wildlife poaching AND protected areas OR reserve OR region name (as above). All online searches for the publications were conducted between 15th November 2014 and 10th March 2015. We screened the returns based on criteria (i-v below) that ensured the results from each paper were related to both PAs and illegal extraction of biodiversity;

- i. Whether the research was done in a protected area and addressed issues of illegal extraction of biodiversity; animals, plants or both.
- ii. Whether the research was on illegal activities by a human population and a mention was clear that the extraction is from the named protected area.
- iii. If the research showed impact on species being extracted, decline or not declined
- iv. Only used primary data papers not meta-analyses or reviews.

123 v. Studies covering similar sites and year of data collection were examined for
124 relevance and only one that satisfied all criteria (i-iii) was included in the
125 analysis.

126 We found no publications that fully satisfied the review criteria for the papers published
127 between 1950 and 1980. Where two or more papers were published for the same protected
128 area during a similar period of data collection, only one that satisfied all the criteria was
129 used for the analysis. From each paper we extracted information on PA location, threat
130 types, study species, perceived impacts of illegal resource use and purpose of research,
131 continent (i.e. Africa, Asia, Europe, South America) and geographic region within
132 continent (i.e. east, central, south and west). We recorded population trend (i.e. decline, no
133 decline or unstated) for each PA/species combination from each paper as reported by the
134 paper and the reasons mentioned for such outcome (e.g. illegal hunting, logging) to
135 examine their effect on population status in the PA. For example, if a paper investigated
136 protected areas X and Y and reported impacts of illegal activities on various species i, j,
137 k..., then each species / site combination became one row in the dataset, including the
138 impact scores (1= species decline or 0 = no decline or NA = no reported impact for that
139 species) and any covariate information for PA or paper (author, year of study, PA name,
140 etc.). The method arriving at the reported population trend status was recorded but not
141 analyzed because most studies did not show the data used to arrive at a species outcome
142 (e.g. decline), thus was difficult to tease apart whether the species decline was causal or
143 correlative, a common problem in many meta-analysis studies (18).

144 Further, we extracted body mass data for each species. For mammals, we used the mammal
145 database PanTHERIA (www.pantheria.org) and the current IUCN species red book data
146 (19). We used body mass of closely-related species for two species that were not located in

147 the mammal database (see supplementary material SM1). Body masses for reptile,
148 amphibian and fish species were either extracted from the original papers (if provided) or
149 from credible online material (supplementary material SM1). For bird body mass we used
150 Dunning (20). To identify the geographical location of the study site, we cross-referenced
151 the papers with the WCMC IUCN Protected Planet database (21) to identify the
152 coordinates of the centroid of each PA. We also searched from this PA database for each
153 name of the researched protected area and recorded its appropriate category under the
154 current IUCN-PA categories.

155 To assess whether population change reported was related to wider scale economic or
156 social change, we extracted country-level human development (HDI) and agricultural land
157 use change (ALC) indices from the UNDP and World Bank databases (22, 23). ALC is an
158 index of measure of the amount of land converted to agriculture and other human activities
159 such as settlement. We calculated the ALC over a decade period encompassing the times
160 when research for the reviewed papers were conducted as most papers did not report the
161 exact dates of data collection. We used HDI as a predictor rather than measures of
162 governance (the two are correlated) because HDI is a more direct indicator of development.
163 Further, to understand the effect of different legal status on species decline we grouped the
164 PAs into two levels of protection: strict PAs (for PAs under IUCN category I & II) and less
165 strict PAs (categories III-VI). Furthermore, we categorized species into two broad groups
166 of mammal and non-mammal for analysis to examine any differences between groups in
167 the way they are threatened by illegal activities. We placed reptile, bird, fish and mollusc
168 into one group: “non-mammal” as data were too sparse for each of these taxa to be tested
169 individually in the model. There was no reported status for any of the plant species in the
170 dataset; therefore, we excluded records of plants from the analysis.

171 **Data analysis**

172 Several papers reported results for many species, and/or information for multiple protected
 173 areas. Here we refer to each unique combination of species within an individual PA (i.e.
 174 species $\times$ PA) reported in a paper as a study, with therefore potentially several studies per
 175 paper (see data extraction in methods). For modelling, we filtered all records where the
 176 population outcome was unknown. We analyzed spatial and temporal trends in research
 177 effort of the previous work on illegal activities and identified existing gaps. To assess
 178 whether population declines are associated with generic factors such as PA level of
 179 protection, type of poaching, species and a country's socio-economic status, we used
 180 generalized linear mixed models (GLMM) with a binomial error term and logit link
 181 function using the statistical software R (version 3.2 R Development Core Team, 2015).

182 We built an initial global model incorporating seven fixed factors: human development
 183 index (HDI), percentage land use change index (ALC), log species body mass, poaching
 184 type (commercial, subsistence, or a mixture), PA level of protection (i.e. IUCN categories
 185 classified as strict and less strict), continent (Africa/Asia/America/Europe) and species
 186 group (i.e. mammal and non-mammal). Because different species could relate to the same
 187 PA and country as studies from other papers at different times, we accounted for this by
 188 including country, paper and PA as random effects in all models and fitted the datasets
 189 using the 'glmer' function implemented in the R-package 'lme4'(24). We used a backwards
 190 stepwise removal of non-significant terms (with Chi-test) to evaluate the relative effect of
 191 each factor on the population decline. We obtained model confidence intervals around
 192 variables showing statistical significance in the minimum adequate model using the Wald-
 193 method (24). Furthermore, in each model we evaluated whether the likelihood of finding an
 194 impact on a species' population was due to the PA level of protection and level of hunting

195 (subsistence, commercial or both) and species group and geographic regions. We also
 196 examined whether log species body size, country's human development index and
 197 agricultural land use change index were consistently correlated with the population decline.
 198 African elephants (i.e. mainly the African savanna elephant *Loxodonta africana*, but with
 199 some data for African forest elephant, *Loxodonta cyclotis*; no data on Indian elephants were
 200 included in the dataset), hereafter referred to as 'elephant', had large numbers of studies in
 201 the dataset (contributing 22 % of all records), probably reflecting the increasing concerns
 202 for its poaching (25). To check the generality of our results, we repeated the analysis using
 203 two subsets of the data: once for elephants alone, and once for all animal species except
 204 African elephants. Similarly, because there were sufficient data to analyze some
 205 components separately we repeated all the analyses with and without the strict PAs (IUCN
 206 categories I&II) as well as on separate subsets of data including Africa and Asia continents
 207 to examine their impact on the whole data set and the relative effects of different predictors
 208 between the two continents.

209

210 **Results**

211 **Spatial distribution and trends in research on poaching in PAs**

212 We identified 1598 papers that met the initial search criteria, of which 92 (Supplementary
 213 material SM2: reporting 1048 species x PA results = 'studies') met all the requirements and
 214 were used for analysis. The 92 published papers researched 146 protected areas from four
 215 continents, with the largest number of studies from Africa and Madagascar (819 studies),
 216 followed by Asia (162), South and Central America (66), and Europe (1) (Figure 1).

217

218 [INSERT FIGURE ONE HERE]

219

220 Figure 1. The locations of all PAs investigated (red dots correspond to centroids of
221 protected areas). Numbers of studies (species x PA combinations) were: Africa and
222 Madagascar (819), Asia (162), South and Central America (66), and Europe (1).

223

224 Most papers focused on single PA (i.e. local scale, n = 54 papers), or few PAs existing as
225 one contiguous ecosystem and landscape (n = 39 papers). All protected area types were
226 investigated but the IUCN category II level of protection was researched the most (57.35%,
227 n = 65 papers; Figure 2). There was no paper published between 1950 and 1979 that
228 satisfied our search criteria: all relevant papers were published in 1980 onwards.

229

230 [INSERT FIGURE TWO HERE]

231

232 Figure 2. The number of studies (species x PA combinations) on illegal activities carried
233 out in PAs with different levels of IUCN protection (I, greatest protection; VI, least). This
234 is based on the 92 papers published between 1980 and 2014, encompassing four continents.
235 There is a strong bias towards the PA category II. The IUCN PA categories are used to
236 facilitate comparisons of different PA ‘entities’ in different countries (e.g. conservation
237 area, forest reserve, game-controlled area, game reserve, game sanctuary, marine reserve,
238 national park and nature reserve).

239

240 The research had varying purposes: investigating impacts (71 papers); conservation
241 rationale (e.g. providing new methods for investigating illegal activities; 17 papers) and
242 management/control of illegal activities (5 papers). Further, research has increased
243 substantially during the last 35 years with greater number of published papers since 2005
244 (Figure S1); most of this increase was in Africa.

245

246 Furthermore, we found a temporal increase in the variety of research methods throughout
247 the period (Figure 3). Interviews (n = 22 papers), animal counts (n = 28) and patrols (n = 9)
248 were the most commonly used methods in the literature. Several research projects (n = 34)
249 combined methods, while two used snare surveys. Animal count was the dominant
250 research method during the first decade (1980-1990) and has increased in use since then.
251 Use of interviewing and patrolling methods to investigate illegal activities in PAs has been
252 used between 1990 and the present (i.e. 2014).

253

254 [INSERT FIGURE THREE HERE]

255

256 Figure 3. Methods used in the 92 publications considered. Recent studies show an
257 increasing diversity of methodological approaches. ‘Other’ includes bone collection from
258 poacher camps and sporadic field observations.

259

260

261 Patterns of species extraction and country socio-economic status

262

Three hundred and fifty-three species, comprising mammals (220), reptiles (18), birds (17), fishes (12), molluscs (2) and plants (84) were reportedly harvested illegally in the 146 protected areas (Table S1). These species were extracted for subsistence use (10.8%, N = 221), commercial use (19.9%) or both (60.6%). Almost nine percent of the studies did not report a reason of illegal resource extraction, and none of the plant studies included all the data that were required for this analysis. The countries where research was conducted showed varying levels of development (Figure 4) and land use change (Figure 5).

270

271 [INSERT FIGURE FOUR HERE]

Figure 4. Human development index (HDI) for the countries where research was conducted. HDI values shown are the mean scores for the total number of years that a country was researched.

275

276 [INSERT FIGURE FIVE HERE]

277

Figure 5. Agricultural land use (ALC) change index of a country where research was conducted. Negative change infers to loss of the natural habitats to agricultural activities and settlement. Mean ALC includes the total number of years a particular country PAs were researched during the last 35 years.

282

283 **Socio-ecological and geographic factors influencing population decline in PAs**
 284 **threatened with illegal activities**
 285
 286 Species body mass and species group (mammal or non-mammal) strongly influenced
 287 probability of species decline in all PA types with species with greater body mass
 288 especially mammals experiencing larger population decline (Model 1 in **Error! Reference**
 289 **source not found.**, Figure 6a). There was an effect of the dominant species in our dataset.
 290 When removed the African elephants, we found that species declines were greater in PAs
 291 faced with commercial rather than subsistence poaching alone (Figure 6b); as before,
 292 mammals and species with greater body mass also exhibited the greatest declines in these
 293 models (Model 2 in **Error! Reference source not found.**).

294

295 Table 1. Results of the GLMM best models showing probability of species decline and the explanatory factors in PAs across four continents.

296 Coefficient sign (+/-) indicates size of effect of covariables i.e. increase for plus and decrease for minus.

297

Type of model and effect size												
Factor in final best model	Model1-all PAs/animal species			Model2-all species/PAs excl. elephants			Model3-strict PAs			Model4-less strict PAs		
	Coefficients + SE	DF	p-value	Coefficients + SE	DF	p-value	Coefficients + SE	DF	p-value	Coefficients + SE	DF	p-value
Species body mass	0.225 ± 0.072	1	0.0013	0.243 ± 0.081	1	0.0018	0.379 ± 0.929	1	0.0001			
Human development index							-8.324 ± 3.526	1	0.0168			
Poaching level (subsist)				-0.221 ± 0.924	3	0.0474						
Poaching level (not given)				0.773 ± 1.496								
Poaching level (commercial)				1.879 ± 1.022								
Agric. land use change index										-2.078 ± 0.739	1	0.0006
Species group (non-mammal)	-1.975 ± 0.910	1	0.0119	-1.792 ± 0.873	1	0.0188	-2.384 ± 1.231	1	0.0161			

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300

301

[INSERT FIGURE SIX HERE]

302

303 Figure 6. Effect of species body mass (a) and level of poaching (b) on the probability of
304 decline of animal species (mammal-upper solid line, and non-mammal-lower dashed line)
305 excluding the dominant species (African elephants) across all PAs (IUCN I-VI). Large
306 bodied species had higher risk of decline when threatened with illegal activities. Shaded
307 area shows 95% CI around the estimates of effect size for the mammal and non-mammal
308 species.

309

310

311 Separate analysis on PAs according to protection level revealed variable results. Human
312 development index (HDI), species body mass and species groups strongly influenced the
313 probability that species would decline in strict PAs (Model 3 in Table 1, Figure 7). Strict
314 PAs in low human development index countries were associated with increased species
315 decline, of mammal species with greater body mass. In contrast, in less strict PAs (IUCN
316 category III-VI), we found species decline was best explained by agricultural land use
317 change (ALC) in the wider area; i.e. species in all PAs with greater habitat loss were more
318 likely to have experienced population decline (Model 4 in Table 1).

319

320

321

[INSERT FIGURE SEVEN HERE]

322

323 Figure 7. HDI influence on population decline of animal species (upper solid line and lower
324 dotted line for mammal and non-mammal respectively) within strict PAs (IUCN category
325 I&II). Least developed countries had the highest probability of their PAs experiencing
326 species decline. Shaded areas show 95% CI around the estimates of effect size of this
327 factor.

328

329

330 The impact of illegal activities on African elephants was variable. Across all PAs (IUCN I-
331 VI), decline was highly associated with lower human development index countries, high
332 habitat loss; i.e. negative agricultural land use change index and with the geographic region
333 of PA location (Model-All PAs in **Error! Reference source not found.**, Figure 8). This
334 decline was greatest in central Africa, followed by the east and west; and least in southern
335 Africa. In an analysis of strict PAs alone we found two factors (i.e. human development
336 index and agricultural land use change index) associated with the increase in elephant
337 decline (Model-strict PAs in Table 2). On the other hand, we found geographic region
338 significantly associated with increased elephant decline within less strict PAs in central and
339 east Africa (Model-less strict PAs in **Error! Reference source not found.**).

340

341

342 Table 2. Results from GLMM models with various factors explaining the probability of decline of African elephants across all PA types and
 343 separately between strict and less strict PAs.

344

Factor in final best model	Type of model and effect size								
	All PAs types (cat. I-VI)			Strict PAs (cat. I & II)			Less strict PAs (cat. III-VI)		
	Coefficients + SE	DF	p- value	Coefficients + SE	DF	p- value	Coefficients + SE	DF	p- value
Human development index	-12.350 ± 4.207	1	0.0005	-19.459 ± 6.496	1	0.0004			
Agri. land use change index	-1.461 ± 0.699	1	0.0116	-1.173 ± 0.826	1	0.0371			
Africa zone (East)	0.723 ± 1.116	3	0.0100				0.406 ± 1.307	3	0.0282
Africa zone (South)	-2.186 ± 1.041						-2.773 ± 1.275		
Africa zone (West)	0.075 ± 2.749						0.981 ± 0.677		

345

346

347 [INSERT FIGURE EIGHT HERE]

348

349 Figure 8. The country's human development index (a) and agricultural land use change
350 index (b) as best predictors of decline in the African elephant within in all PAs (category I-
351 VI) across the African continent. High negative ALC values are associated with severe
352 habitat loss and a high risk of population decline of African elephants. Gray area shows
353 95% CI around the estimates in the minimum adequate GLMM model.

354

355

356 Furthermore, the probability that illegal activities were associated with population declines
357 also varied regionally across PAs in Africa, Asia and Latin America. Lower human
358 development index of countries, greater species body mass and species group (i.e.
359 mammal) were the strongest predictors of increased species decline in PAs across Africa
360 (Model -Africa in **Error! Reference source not found.**). In contrast, species decline in
361 Asia was strongly positively associated with PA strictness (Model-Asia in Table 3). On the
362 combined data for Asia and Latin America, we found that increased probability of species
363 decline in PAs across these continents was correlated with greater agricultural land use
364 change (Model combined in **Error! Reference source not found.**).

365

366 Table 3. Results from GLMM models with influence of the various factors on the probability of species decline in PAs separately for Africa
 367 and Asia continents and on combined data for Asia and Latin America.

368

Type of model and effect size									
Factor in final best model	Africa-all animals/PAs			Asia-all animals/PAs			Asia + L. America		
	Coefficients + SE	DF	p-value	Coefficients + SE	DF	p-value	Coefficients + SE	DF	p-value
Human development index	-8.657 ± 3.708	1	0.00386						
Body mass	0.338 ± 0.084	1	0.00022						
Species group (non-mammal)	-2.269 ± 1.095	1	0.01223						
PA strictness				1.974 ± 0.684	1	0.0237			
Agric. land use change index							-13.946 ± 4.741	1	0.0077

369

370

371 Discussion

372 Biodiversity in protected areas faces numerous anthropogenic threats (11). We analyzed
 373 data published since the 1980's to understand impacts of illegal activities on species decline
 374 in protected areas. There were a strong taxonomic and geographic biases in research on
 375 illegal activities within protected areas during the review period. We found that population
 376 declines were more likely consequences of illegal activities in countries with low human
 377 development index (HDI). Different groups of species declined at different rates, with large
 378 bodied mammals mostly likely to show population decline. As well as poaching, we also
 379 found that habitat loss had an additional impact on population decline of animal species in
 380 less strict PAs, particularly in countries experiencing greater agricultural land use change.
 381 Further, species decline was also associated with geographic region of PA location being
 382 greater in Africa than Asia or Latin America.

383 The identification of correlations between human development indices and illegal activities
 384 in this study supports a widely held view, e.g. Bennett, Blencowe (26), Adams, Aveling
 385 (27), but one that is often based on limited data (28): that biodiversity decline is greater in
 386 relatively poor regions. Low human development scores could impact illegal activities in
 387 two ways: firstly, poor people may tend to exploit species illegally from PAs because they
 388 have limited alternatives (29). Secondly, poor countries have fewer resources to invest in
 389 PA conservation. Underfunding may result in increased illegal activities in PAs due to
 390 insufficient law enforcement (30). This is supported by our model encompassing the most
 391 strictly protected areas alone, which indicates high probability of species decline associated
 392 with low human development index countries (Table 1). Hilborn, Arcese (31) demonstrated
 393 that increased funding budgets for anti-poaching activities in the Serengeti National park
 394 greatly reduced poaching pressures and lead to the recovery of the buffalo population.

395 However, increasing conservation funding may not necessarily result into improved
 396 conservation particularly when social and political constraints exist. For example, social
 397 and political unrest may increase rates of illegal activities, reduce wildlife populations and
 398 thwart conservation efforts altogether (32, 33). Our results provide evidence that poverty, in
 399 as much as it is measured by the HDI, may have significant negative impacts on species
 400 due to accelerated poaching, whether that be because of increased external pressures on
 401 PAs or decreased policing and protection within strict PAs. Further, illegal activities
 402 increased species vulnerability to decline through increased habitat loss mostly in less
 403 strictly protected areas (Table 1). This could be because these PAs are often afforded
 404 minimal protection (34) and therefore this exposes them to intense illegal activities making
 405 them less reliable for the effective conservation of large and medium-size mammals (35).
 406 These findings also provide evidence that supports Craigie et al.'s (2010) assertions that
 407 illegal hunting and habitat loss are the major causes of continental-wide declines in
 408 megafauna in PAs across Africa. Our study highlights the need to consider human
 409 development issues more seriously to ensure effective conservation of biodiversity within
 410 existing protected areas.

411 Large bodied species are likely highly susceptible to decline because they have slow
 412 growth rates and so overharvesting is likely to cause population decline (36). Low
 413 population growth rates in combination with multiple threats from poaching and diseases
 414 are known to have significant impact on population persistence (12, 15). By contrast,
 415 smaller mammals (with higher reproductive and growth rates) showed fewer declines and
 416 appeared to sustain harvest, though relatively few small species are the specific targets of
 417 poaching in the PAs. Our model that excluded elephant suggested that commercial
 418 poaching has the greatest potential to cause population decline. Further, the propensity for

419 elephants to decline in low human development index countries and geographic regions,
420 and where habitat loss was taking place (Table 3), is consistent with recent analyses that
421 this species is threatened with poaching and habitat loss across its habitat range in Africa
422 (37, 38).

423 The pattern of species declines across the network of protected areas is worrying and
424 suggests that PA policing (including access to appropriate conservation information) and
425 resources need to be improved. PA-specific information is important for understanding how
426 illegal activities vary spatially and across time and there is a need to be able to predict
427 future trends and thereby possible future management strategies e.g. Critchlow, Plumptre
428 (39). Furthermore, land use change poses additional risks of species decline in PAs across
429 Asia and Latin America, relative to Africa, and its impact was more severe in less strict
430 than strict PAs (**Error! Reference source not found.**). This could be attributable to the
431 habitat loss and poaching occurring inside these protected (40-42), or the wider effects on
432 animals that roam outside protected areas for parts of the year. These results are consistent
433 with previous studies that have reported biodiversity decline and loss within PAs in these
434 regions e.g. Geldmann, Barnes (16), Harrison (43), Laurance, Carolina Useche (44). Our
435 findings suggest that land use change is a major threat that requires urgent attention to
436 improve PA conservation across Latin America and continental Asia.

437 The geographical bias in the spatial distribution of research observed in these data is likely
438 a consequence of interests among the researchers rather than being driven solely by the
439 levels of illegal activities in particular PAs or countries. However, the temporal and spatial
440 patterns of research observed in this study provide insight into the extent of the problem of
441 illegal activities in PAs and therefore suggest that PAs are currently in need of new
442 strategies to minimize impacts of illegal activities and to improve their conservation

effectiveness (45). To date, research effort has concentrated on quantifying the extent and impact of illegal activities on focal species; in other words, documenting the problem. Far less information is available on which conservation management strategies (including human development and preventing illegal international trade, as well as within-PA activities) are most effective at reducing illegal activities. Only 5 out of 92 publications reviewed here explicitly considered how the management of illegal activities might affect population declines. New research should focus on developing and testing new methods for reducing levels and impacts of illegal activities on species in PAs.

Conclusion

Tackling illegal activities within protected areas remains a high conservation priority. Our results suggest that a combination of strategies may be required that simultaneously reduce the frequency with which illegal activities are attempted and reduce the likelihood that such attempts will be successful (from the perspective of the perpetrators). Regarding the former, we found that illegal activities in poor countries often lead to population declines within PAs. These findings suggest that poverty alleviation may be an appropriate conservation strategy to reduce illegal activity pressures (26). The implication of this for local and national policies is that more effort needs to be invested to improve the social and economic status of the human populations. This needs to work in tandem with increasing the effectiveness of traditional conservation activities to prevent illegal activities; which may itself reduce the inclination of people to attempt future illegal activities. At the international level, these results may imply that PAs in low HDI countries may need more international support to curb pressures of illegal activities, particularly those driven by trans-boundary forces. Sound strategies to stop elephant poaching and ivory trade, and trade

466 in bushmeat, as well as strengthening collaboration in conservation and research, are
467 necessary to improve PA effectiveness in these countries.

468

469 **Acknowledgements**

470 We are grateful to the anonymous reviewers for the comments on earlier drafts of this
471 manuscript. AAR is a commonwealth scholar funded by the U.K. government.

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598 SUPPORTING INFORMATION CAPTIONS

599 Table S1. The reasons recorded by the studies to explain the status of biodiversity reported
600 in the reviewed papers. Plus (+) sign indicates the reason was mentioned together with the
601 poaching in the PA. Studies (43.2%, n = 453) that sum up to the totals did not indicate the
602 status of species being investigated and are not shown here.

603

604 Figure S1. Increasing publication trend for illegal activities in PAs during the last 35 years.

605

606 Table S2. 353 species extracted and threatened with illegal activities in 146 PAs across four
607 continents as published in the last 35 years (1980-2014)

608

609 SM1: List of Additional Sources of data for Species body mass

610

611 SM2: Bibliography of the 92 research papers used in this analysis

612

613

614

LIST OF FIGURES

Figure 1

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Figure 2

Figure 3

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Figure 6

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Figure 7

Figure 8