The global decline of cheetah *Acinonyx jubatus* and what it means for conservation

Sarah M. Durant[a,b,c,1], Nicholas Mitchell[a,b], Rosemary Groom[a,b], Nathalie Pettorelli[a,c], Audrey Ipavec[a,b], Andrew P. Jacobson[a,d], Rosie Woodroffe[a,c], Monika Böhm[a,c], Luke T. B. Hunter[e], Matthew S. Becker[f,g], Femke Broekhuis[h,i], Sultana Bashir[a], Leah Andresen[j], Ortwin Aschenborn[k], Mohammed Beddiaf[l], Farid Belbachir[m], Amel Belbachir-Bazi[m], Ali Berbash[n], Iracelma Brandao de Matos Machado[o], Christine Breitenmoser[p,q], Monica Chege[r], Deon Cilliers[s], Harriet Davies-Mostert[t], Amy J. Dickman[h], Fabiano Ezekiel[u], Mohammad S. Farhadinia[h], Paul Funston[e], Philipp Henschel[e], Jane Horgan[v], Hans H. de Iongh[w], Houman Jowkar[x,y], Rebecca Klein[v], Peter Andrew Lindsey[e], Laurie Marker[z], Kelly Marnewick[t], Joerg Melzheimer[aa], Johnathan Merkle[f], Jassiel M'soka[bb], Maurus Msuha[cc], Helen O'Neill[a,c], Megan Parker[dd], Gianetta Purchase[a], Samaila Sahailou[ee], Yohanna Saidu[ff], Abdoulkarim Samna[ee], Anne Schmidt-Küntzel[z], Eda Selebatso[gg], Etotépé A. Sogbohossou[hh], Alaaeldin Soultan[ii], Emma Stone[jj], Esther van der Meer[kk], Rudie van Vuuren[ll], Mary Wykstra[mm], and Kim Young-Overton[e]

[a]Institute of Zoology, Zoological Society of London, London NW1 4RY, United Kingdom; [b]Wildlife Conservation Society, New York, NY 10460; [c]Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, United Kingdom; [d]Department of Geography, University College London, London WC1E 6BT, United Kingdom; [e]Panthera, New York, NY 10018; [f]Zambian Carnivore Programme, Mfuwe, Zambia; [g]Conservation Biology and Ecology Program, Department of Ecology, Montana State University, Bozeman, MT 59717; [h]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford OX13 5QL, United Kingdom; [i]Mara Cheetah Project, Kenya Wildlife Trust, Kenya; [j]Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth 6031, South Africa; [k]Bwabwata Ecological Institute, Susuwe Park Station, Zambezi Region, Ministry of Environment and Tourism, Namibia; [l]Office National du Parc Culturel du Tassili N'Ajjer, Djanet, Algeria; [m]Laboratoire d'Écologie et Environnement, Université de Béjaïa, Béjaïa, Algeria; [n]Nature Conservation Department, Environment General Authority (EGA), Tripoli, Libya; [o]Institute of Veterinary Services, Ministry of Agriculture, Luanda, Angola; [p] Carnivore Ecology and Wildlife Management (KORA), 3074 Muri, Switzerland; [q]International Union for the Conservation of Nature/Species Survival Commission Cat Specialist Group, 3074 Muri, Switzerland; [r]Kenya Wildlife Service, 00100 Nairobi, Kenya; [s]Cheetah Outreach Trust, Paardevlei, South Africa; [t]Endangered Wildlife Trust, Johannesburg, South Africa; [u]Department of Wildlife Management and Ecotourism, University of Namibia, Windhoek, Namibia; [v]Cheetah Conservation Botswana, Gaborone, Botswana; [w]Institute of Environmental Sciences, Leiden University, 2300 RA Leiden, The Netherlands; [x]Persian Wildlife Heritage Foundation, Tehran 15856-86341, Iran; [y]Conservation of Asiatic Cheetah Program, Department of Environment, Tehran, Iran; [z]Cheetah Conservation Fund, Otjiwarongo, Namibia; [aa]Department Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, 10315 Berlin, Germany; [bb]Department of National Parks and Wildlife, Chilanga, Zambia; [cc]Tanzania Wildlife Research Institute, Arusha, Tanzania; [dd]Working Dogs for Conservation, Bozeman, MT 59771; [ee]Direction de la Faune, de la Chasse et des Aires Protégées, Niamey, Niger; [ff]Nigeria National Park Service, Garki, Abuja, Nigeria; [gg]Consultant, Gaborone, Botswana; [hh]Laboratory of Applied Ecology, University of Abomey-Calavi, Cotonou, Benin; [ii]Egyptian Environmental Affairs Agency, Cairo, Egypt; [jj]Carnivore Research Malawi, Conservation Research Africa, Lilongwe, Malawi; [kk]Cheetah Conservation Project Zimbabwe, Victoria Falls, Zimbabwe; [ll]Naankuse Foundation, Windhoek, Namibia; and [mm]Action for Cheetahs in Kenya, Nairobi, Kenya

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Establishing and maintaining protected areas (PAs) are key tools for biodiversity conservation. However, this approach is insufficient for many species, particularly those that are wide-ranging and sparse. The cheetah *Acinonyx jubatus* exemplifies such a species and faces extreme challenges to its survival. Here, we show that the global population is estimated at ∼7,100 individuals and confined to 9% of its historical distributional range. However, the majority of current range (77%) occurs outside of PAs, where the species faces multiple threats. Scenario modeling shows that, where growth rates are suppressed outside PAs, extinction rates increase rapidly as the proportion of population protected declines. Sensitivity analysis shows that growth rates within PAs have to be high if they are to compensate for declines outside. Susceptibility of cheetah to rapid decline is evidenced by recent rapid contraction in range, supporting an uplisting of the International Union for the Conservation of Nature (IUCN) Red List threat assessment to endangered. Our results are applicable to other protection-reliant species, which may be subject to systematic underestimation of threat when there is insufficient information outside PAs. Ultimately, conserving many of these species necessitates a paradigm shift in conservation toward a holistic approach that incentivizes protection and promotes sustainable human–wildlife coexistence across large multiple-use landscapes.

population viability analysis | threat assessment | protected areas | landscape conservation | megafauna

The spread and dominance of humans across the world during the Anthropocene have precipitated a sixth global biodiversity extinction crisis (1). To maximize biodiversity retention through this period of rapid change, scarce conservation resources need to be targeted toward species and ecosystems that are most

Significance

Here, we compile and present the most comprehensive data available on cheetah distribution and status. Our analysis shows dramatic declines of cheetah across its distributional range. Most cheetah occur outside protected areas, where they are exposed to multiple threats, but there is little information on population status. Simulation modeling shows that, where cheetah population growth rates are suppressed outside protected areas, extinction risk increases markedly. This result can be generalized to other "protection-reliant" species, and a decision tree is provided to improve their extinction risk estimation. Ultimately, the persistence of protection-reliant species depends on their survival outside and inside protected areas and requires a holistic approach to conservation that engages rather than alienates local communities.

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[1]To whom correspondence should be addressed. Email: s.durant@ucl.ac.uk.

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threatened. However, in the absence of complete information, reliable assessment of threat is challenging. The International Union for the Conservation of Nature (IUCN) Red List criteria are the primary tools for identifying and categorizing species-based extinction risk, enabling prioritization of species facing the highest threat (2). However, much of the information used for assessment comes from relatively well-monitored populations, usually within protected areas (PAs) (3), although across a species' distributional range, populations are likely to be exposed to variable threat levels and differing management regimes (4).

Inaccuracies in threat assessment are particularly problematic for large terrestrial mammals, which can be especially vulnerable to anthropogenic impacts, such as habitat loss and fragmentation, human–wildlife conflict, illegal wildlife trade, and overharvesting for bushmeat or traditional use (5–7). These threats are usually higher outside PAs, leading to systematic spatial variation in population status according to levels of protection. However, this spatial variation may go undetected if information on population status and trends is biased toward relatively high-density populations, often found within PAs (3). Such biases are widespread, because wildlife management authorities may be required to monitor wildlife within PAs but not outside them, and monitoring is usually more challenging outside PAs, because wildlife are more elusive and occur there at lower densities (8, 9). This deficit leads to a lack of information on populations outside PAs, where they are generally more threatened, resulting in an overly favorable assessment of status.

Results

Cheetah Status and Threat Assessment. The cheetah *Acinonyx jubatus* is a large carnivore that faces particularly acute challenges during the Anthropocene. It is one of the most wide-ranging carnivores, with home ranges documented in excess of 3,000 km^2 (10, 11) and movements of translocated animals exceeding 1,000 km (11). However, densities seldom exceed 0.02/km^2 and have been recorded as low as 0.0002/km^2 (12).

Historically widespread across Africa and southwestern Asia, cheetah are now known to occur in only 9% of their past distributional range (Fig. 1). Not only has there been a worrying contraction in global cheetah range, but current range is extremely fragmented. The global population is tentatively estimated at around 7,100 adult and adolescent cheetah distributed across 33 populations (Table 1). More than one-half of the world's cheetah occur in a single transboundary population stretching across six countries in southern Africa (Table 1). Only one other population comprises more than 1,000 individuals, and most populations (91%) comprise 200 individuals or fewer. Six populations do not even reach double digits. Ongoing population trends are largely unknown; however, of 18 populations where trends could be assigned, 14 were judged to be in decline, 3 were stable, and only 1 was stable or increasing (Table 1).

In Asia, the decline of cheetah has been particularly precipitous. Cheetah have been extirpated from 98% of their historical range, and a critically endangered population of Asiatic cheetah *Acinonyx jubatus venaticus* survives only in Iran (Table 1). This remnant population is tentatively estimated to comprise fewer than 50 individuals distributed across three core areas of range (13). The rest of the world's cheetah occur in Africa, spread across 30 fragmented populations that are now restricted to only 13% of their historical distributional range (14–16) (Fig. 1 and Table 1).

Across their surviving range, cheetah populations vary in the level of threat that they experience. Most resident range (77%) is on unprotected land, which supports an estimated 67% of the cheetah population (Table 1). Here, cheetah face increased pressures from widespread human–wildlife conflict, prey loss caused by overhunting and bushmeat harvesting, habitat loss and fragmentation, and illegal trade (14–16). The species thus faces spatially heterogeneous threats that are higher outside than inside PAs, whereas much of the data available for threat assessment comes from within PAs, which support the highest reported densities of cheetah (~0.02/km^2) (17, 18). Populations on unprotected lands and in small or poorly managed PAs, where they are exposed to multiple threats, are likely to be in decline. However, because of the considerable survey and monitoring effort required, particularly for a wide-ranging and elusive species like the cheetah, such declines are likely to go undetected.

Protection and Extinction Risk. Spatial variation in threat across protection gradients in a species' range is expected to affect overall extinction risk. To assess these impacts for cheetah, we used scenario modeling to (*i*) explore the relationship between extinction risk and population size while varying both the proportion of land protected and the growth rate on unprotected lands and (*ii*) predict population trends. We assumed that populations were stable when protected, which is observed in large PAs (19). Our model revealed markedly higher extinction probabilities when the percentage of land under protection was low and when growth rates outside PAs were less than replacement (Fig. 2). When there was no migration or medium migration (5% of the subpopulation per annum) between protected and unprotected land, there was a rapid

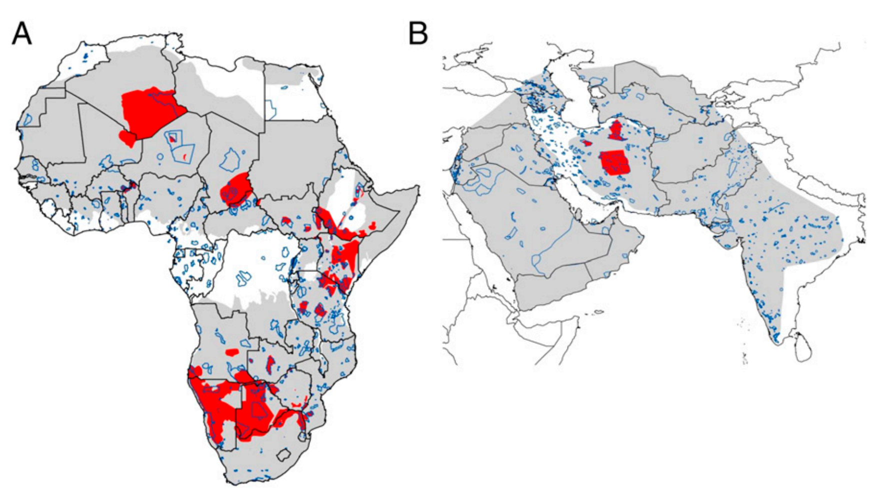

Fig. 1. Known cheetah distribution in (*A*) Africa and (*B*) Asia. Gray shading denotes historical range, and red shading shows the range where cheetah are known to be resident. Boundaries of PAs under IUCN categories I–IV are marked in blue.

Table 1. Summary of known cheetah distributional range and populations

Area name	Countries	Resident range (km^2)	Population size	Overall increase/stable/decrease*	Resident range in PAs	Range in PAs (%)	Population size in PAs	Population in PAs (%)
Africa								
Southern Africa six-country polygon	Angola/Botswana/Mozambique/Namibia/South Africa/Zambia	1,212,179	4,021	↓	283,851	23.4	1,041	25.9
Moxico	Angola	25,717	26	?	0	0.0	0	0.0
Pandmatenga/Hwange/Victoria Falls	Botswana/Zimbabwe	25,926	50	↓	15,551	60.0	29	58.0
Banhine	Mozambique	7,266	10	?	0	0.0	0	0.0
Malilangwe/Save/Gonarezhou	Mozambique/Zimbabwe	9,922	46	↔	4,757	47.9	19	41.3
Kafue	Zambia	26,222	65	?	22,185	84.6	55	84.6
Liuwa	Zambia	3,170	20	↑ or ↔	2,921	92.1	18	90.0
Bubyana, Nuanetsi, and Bubye Conservancies	Zimbabwe	8,816	40	↓	0	0.0	0	0.0
Zambezi valley	Zimbabwe	3,612	12	↓	2,102	58.2	7	58.3
Matusadona	Zimbabwe	1,422	3	↓	1,422	100.0	3	100.0
Midlands Rhino Conservancy	Zimbabwe	318	4	↓	0	0.0	0	0.0
Subtotal southern Africa		1,324,570	4,297		332,789	25.1	1,172	27.3
Afar	Ethiopia	4,480	11	↓	1,092	24.4	3	27.3
Blen-Afar	Ethiopia	8,170	20	↓	1,856	22.7	5	25.0
Ogaden	Ethiopia	12,605	32	↓	0	0.0	0	0.0
Yangudi Rassa	Ethiopia	3,046	8	↓	3,046	100.0	8	100.0
Kenya/Ethiopia/South Sudan	Ethiopia/Kenya/South Sudan	191,180	191	?	37,953	19.9	38	19.9
South Turkana	Kenya	3,580	36	?	1,117	31.2	11	30.6
Kidepo/southern South Sudan/northwest Kenya	Kenya/South Sudan/Uganda	6,694	19	?	1,422	21.2	4	21.1
Serengeti/Mara/Tsavo/Laikipia/Samburu	Kenya/Tanzania	280,114	1,362	↓	49,705	17.7	664	48.8
Badingilo NP	South Sudan	8,517	85	?	4,741	55.7	47	55.3
Radom NP	South Sudan	6,821	68	?	0	0.0	0	0.0
Southern NP	South Sudan	14,680	147	?	10,863	74.0	109	74.1
Ruaha ecosystem	Tanzania	30,820	200	↔	25,551	82.9	166	83.0
Maasai Steppe	Tanzania	20,409	51	↓	3,755	18.4	9	17.6
Katavi-Ugalla	Tanzania	23,955	60	?	10,475	43.7	26	43.3
Subtotal eastern Africa		615,071	2,290		151,576	24.6	1,090	47.6
Adrar des Ifoghas/Ahaggar/Ajjer and Mali	Algeria/Mali	762,871	191	?	98,867	13.0	25	13.0
WAP	Benin/Burkina Faso/Niger	25,345	25	?	20,923	82.6	21	82.6
CAR/Chad	CAR/Chad	238,234	238	?	44,396	18.6	44	18.6
Termit Massif	Niger	2,820	1	?	2,820	100.0	1	100.0
Air and Ténéré	Niger	8,052	2	?	8,052	100.0	2	100.0
Subtotal western, central, and northern Africa		1,037,322	457		175,058	16.9	93	20.3
Total Africa		2,976,963	7,044		659,423	22.2	2,355	33.4
Asia								
Southern landscape	Iran	107,566	20	↔	41158	38.3	N/A	N/A
Northern landscape	Iran	33,445	22	↓	18077	54.04	N/A	N/A
Kavir	Iran	5,856	1	↓	5,856	100.0	N/A	N/A
Total Asia		146,867	43		65,091	44.3	N/A	N/A
Total global		3,123,830	7,087		724,514	23.2	2,355†	33.4†

Historical distributional range for cheetah totals 33,056,767 km^2, comprising 23,340,522-km^2 African range and 9,716,245-km^2 Asian range (Fig. 1). CAR, Central African Republic; N/A, not applicable; NP, National Park; WAP, W, Arly and Pendjari protected area complex; ↓, decrease; ↑, increase; ↔, stable.
*Estimates of trend apply to the entire polygon; thus, for example, populations may increase at specific sites, although there is an overall decrease across the polygon.
†Does not include Iranian cheetah.

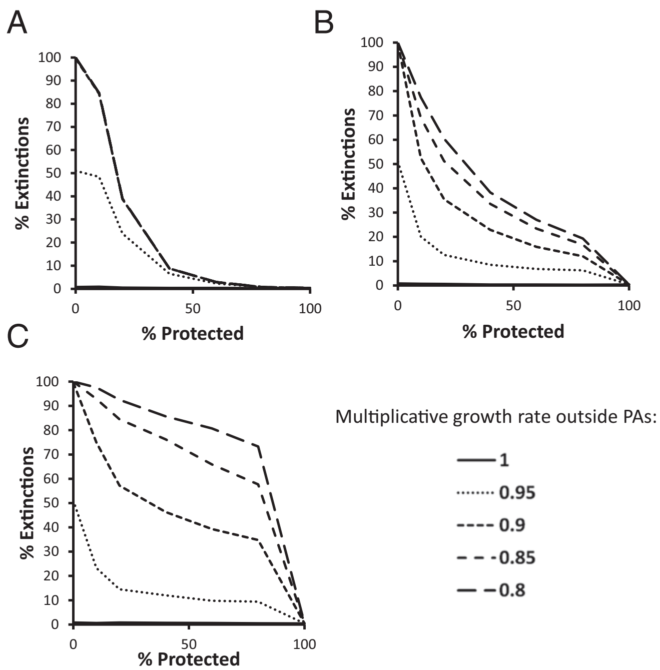

Fig. 2. Scenario modeling of a population of cheetah living on unprotected and protected lands. Starting population is 200 individuals distributed at a varying proportion between protected and unprotected lands (*x* axis). Multiplicative growth rate (lambda) inside PAs is 1.0, but outside PAs, it is allowed to vary from this rate down to 0.8. Graphs show estimated extinction rates under three migration scenarios: (*A*) no migration between protected and unprotected lands, (*B*) medium migration rate between protected and unprotected lands of 0.05 and SD of 0.025, and (*C*) high migration rate of 0.1 and SD of 0.05. Results are reported from 1,000 simulations over 50 y.

increase in extinction rate when the proportion of land protected dropped below 40% (Fig. 2 *A* and *B*). When the migration rate was high (10% of the subpopulation per annum), extinction rate was high, even when 80% of the population was protected and the reduction in growth rate outside PAs was modest (Fig. 2*C*). Long-term studies of cheetah suggest that migration rates of between 5 and 10% are likely to be realistic (*Materials and Methods*).

We simulated the global cheetah population by setting the initial population equal to the estimated population of 7,000 individuals, of which 33% occurs in PAs (Table 1). When the population growth rate outside PAs was 10% less than replacement and migration rate was 5% of the subpopulation per annum, simulated populations declined by 53% over 15 y or three cheetah generations (Fig. 3*A*). When the growth rate outside PAs was 20% less than replacement, then the decline was 70%. Changing the migration rate had little effect on overall population decline (Fig. S1). If the growth rate inside PAs is above replacement, then this slows the rate of decline; however, growth rates need to be high to completely mitigate against declines (Fig. 3*B* and Fig. S2).

Evidence of recent cheetah population declines is consistent with modeling results. For example, in Zimbabwe, where cheetah distribution is relatively well-known, cheetah were distributed across a contiguous population encompassing 132,931 km^2 in 2007, which contracted to a fragmented population occupying only 49,124 km^2 by 2015 (16, 20, 21). This 63% range contraction over a short period, equivalent to a loss of 11% of distributional range per year, was largely because of the disappearance of cheetah outside PAs associated with major changes in land tenure (22). The Zimbabwean cheetah population is also estimated to have declined by at least 85% between 1999 and 2015 (20), equivalent to an annual decline of 13%. Similarly, there have been recent large-scale extinctions of cheetah across western and central Africa (23, 24). Ongoing rapid change is likely across the African continent because of changes in land tenure (22), large-scale fencing (25), land grabs (26), and political instability (27). However, cheetah status in areas where they are most threatened is usually uncertain, because those areas lack data. On this basis, in line with the precautionary approach and in the absence of alternative information, our analysis suggests that cheetah should be uplisted to endangered under IUCN Red List criterion A3b (28).

Protection-Reliant Species. Our model is generic, depending primarily on data on the mean and variance of the growth rate, and shows that extinction risk can be seriously underestimated if differences in population growth rates on protected and unprotected land are not taken into account. We assumed two panmictic subpopulations: one protected and one unprotected. In reality, populations are likely to be much more fragmented, which increases extinction risk, because small isolated populations are more extinction-prone than large connected ones (29). We also assumed that the PA subpopulation was stable and hence, unable to compensate for pressures on unprotected populations. This assumption may hold for many large mammal species. Indeed, given widespread evidence of wildlife declines in many PAs (30), our assumption of stability may even be overly optimistic. If populations are able to grow inside PAs, this increase will help mitigate against declines outside PAs; however, growth rates in excess of 8% per annum inside PAs are needed to counteract a decline of more than 10% per annum outside PAs (Fig. 3*B*).

There is growing evidence that many populations are subject to source–sink dynamics, whereby protected source populations may supplement declining sink populations (31). Our results show that, when sources are unable to mitigate against declines, then there may be catastrophic consequences on populations. Populations of wide-ranging species are particularly vulnerable to edge effects on PA boundaries, which will damage their capacity to act as sources and compensate for sinks outside (32). Worryingly, there is also increasing evidence for exacerbated sink effects or "ecological traps," where species are attracted to sinks or "traps" that may be outside PAs, either because they harbor important resources or to avoid competition or predation (33).

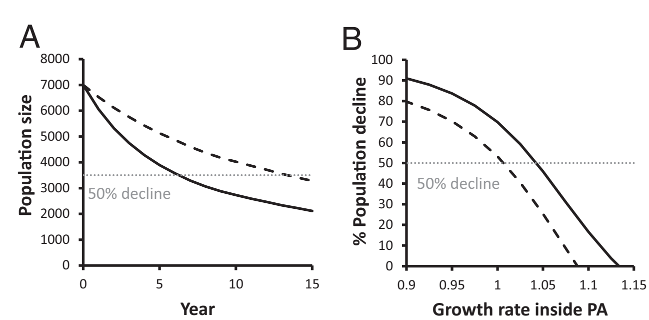

Fig. 3. Simulated (*A*) population trajectories over three generations (15 y) of the global cheetah population and (*B*) sensitivity analysis to changes in the growth rate within PAs. Starting population was the current total estimated global population size of 7,000 individuals, with 33% of the population on protected lands (Table 1). The dashed lines depict results from a multiplicative growth rate (lambda) of 0.9 on unprotected lands, and the solid lines show 0.8. Migration rate was set at 0.05 with SD of 0.025. Results are reported from 1,000 simulations, and all other parameters of the model are as described for Fig. 2. The gray dotted lines depict the 50% threshold for uplisting to endangered status using the IUCN Red List criterion A3b [a population size reduction of ≥50% projected or suspected to be met within the next three generations based on an index of abundance (28)].

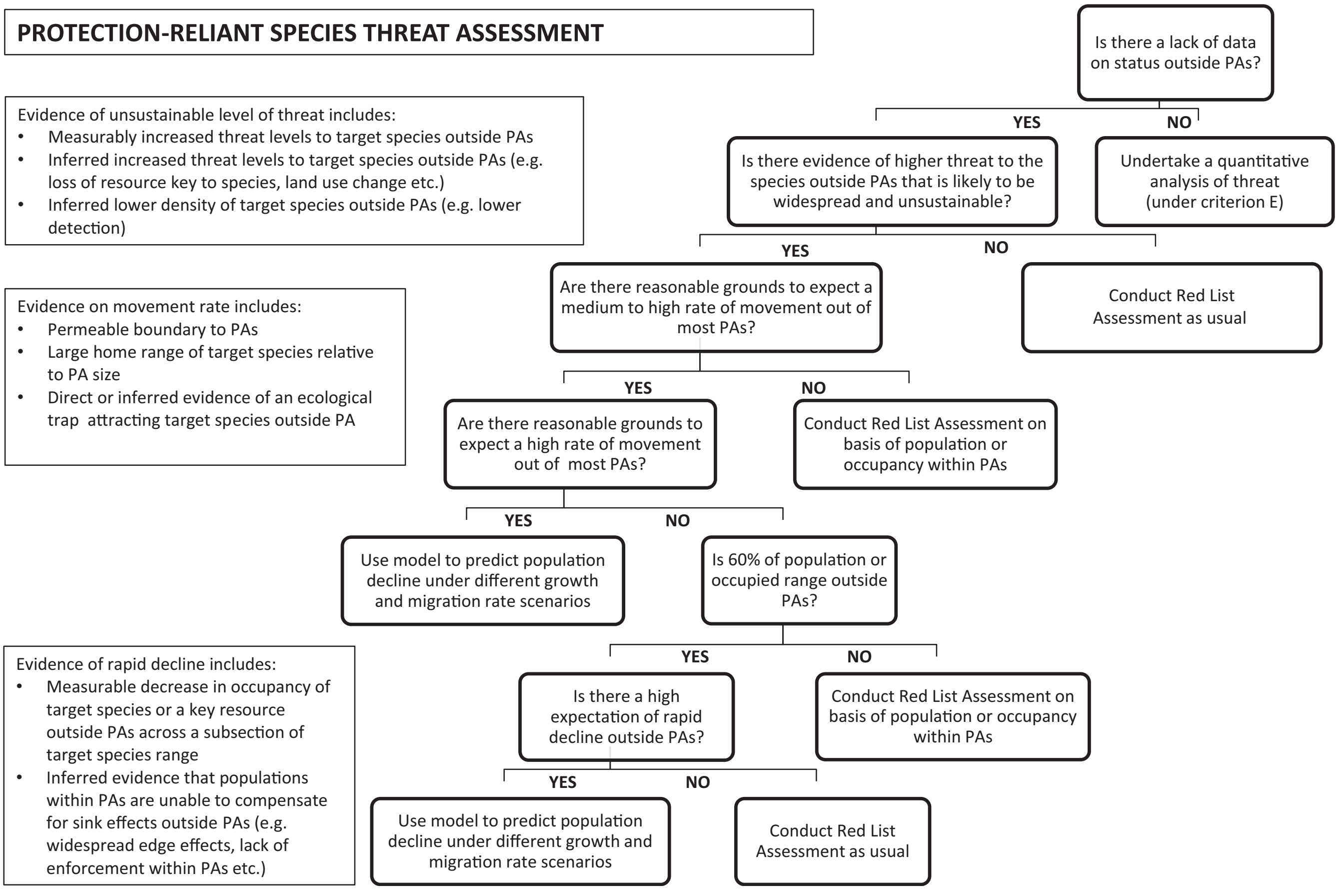

Fig. 4. Decision tree for threat assessment of protection-reliant species.

Accordingly, our modeling scenarios are not unrealistic, and results may be generalized to those other large mammal species that are assessed to be protection-reliant. Such species may have substantial range outside PAs but are vulnerable to rapid anthropogenic change, which results in populations outside PAs acting as sinks. Our analysis shows that assessment of threat may be underestimated for protection-reliant species, requiring urgent reassessment of extinction risk. We provide a decision tree to assist this assessment process based on our simulation results that takes account of the proportion of distribution or population outside PAs and evidence on threats (Fig. 4). The term protection-reliant differs in important respects from the conservation-dependent subcategory within the lower-risk category used in the IUCN Red List until 2001 (34). Conservation-dependent species are not threatened but might be so if conservation measures are withdrawn. By contrast, protection-reliant species may often be threatened and additionally, face elevated risks of extinction because of increased pressures outside PAs, where a substantial proportion of their population persists.

Clearly, an accurate assessment of threat is a key step in identifying those protection-reliant species that are most vulnerable to extinction; however, for some species, the PA system may be insufficient to secure long-term survival. In the case of cheetah, PAs support only an estimated 2,360 individuals, and many PAs are too small to sustain populations that are viable in the long term. For such protection-reliant species, a different approach may be needed to halt declines outside PAs and reduce impacts of edge effects on populations inside PAs to maintain connectivity and secure long-term viability of populations across large multiple-use landscapes. Although some have advocated fencing to reduce edge effects, such interventions are likely to have considerable negative impacts on ecosystems and communities, whereas the massive areas required for wide-ranging species, like cheetah, make the costs prohibitive (25).

Our analysis shows that growth rates within PAs have to be unrealistically high to fully compensate for declining populations outside PAs (Fig. 3*B*); thus, protection-reliant species are likely to respond better to an approach focused on increasing their growth rates on unprotected lands. Thus, safeguarding protection-reliant species, like cheetah, may require a paradigm shift in conservation away from a primary focus on protection toward a holistic framework that additionally incorporates incentive-based approaches (35). For this shift to occur, new policy, management, and financial tools are needed that promote coexistence between people and wildlife outside and adjacent to PAs (36). This innovation will require concerted action from governments and effective cross-sectoral engagement across the conservation and economic development communities. Securing sustainable solutions for wildlife and people will not be easy, particularly where threatened species may share their range with marginalized and vulnerable communities and where human development challenges are substantial. However, unless this transformation is achieved, the future of wide-ranging and highly threatened species, such as cheetah, is in doubt.

Materials and Methods

Assessing Cheetah Distribution and Status. Distributional mapping of cheetah in Africa used an expert-based mapping approach established for jaguar and tiger (37, 38) during IUCN/Species Survival Commission conservation strategic planning workshops for cheetah and another similarly sparse and wide-ranging species, African wild dog *Lycaon pictus* (14–16, 21). Additional map refinements were conducted during National Conservation Action or Management Planning Workshops and from published reports and scientific articles. Mapping in Asia was conducted by a small expert team comprising L.T.B.H., M.S.F., and H.J. using information from ongoing survey work in Iran and the IUCN Red List assessment for the Asian subspecies (13, 39). Resident range was defined as land where the species was known to be still resident as recognized by (*i*) regular detection of the species in an area over a period of several years and/or (*ii*) evidence of breeding. Population size for each resident range polygon was estimated either from expert knowledge (based on surveys and monitoring) or using known densities from populations in comparable habitats facing similar levels of threat (14–16, 21, 28). Trends for each polygon were assigned as increasing, decreasing, stable, or unknown based on the expert judgement of those working at sites within polygons.

Simulation Modeling. Population simulations were conducted in R (40). Mean and SD in the multiplicative growth rate (lambda) in PAs were set at the values observed in the female cheetah population in the Serengeti National Park from 1982 to 2011 (19) (i.e., with a mean of 1.0 and an SD of 0.13). These growth rate parameters implicitly include the impacts of competitors [such as lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*)] on overall growth rate, because both of these predators were present in this PA. Even in well-managed PAs, high cub mortality because of predation may prevent cheetah populations from achieving lambda > 1 (41). Outside PAs, mean lambda was allowed to vary from 1 to 0.8, with the SD set to the same value as within PAs (0.13). For each year, growth rates inside and outside PAs were randomly chosen from a normal distribution.

Migration between subpopulations on protected and unprotected lands was assumed to be proportionate to each subpopulation, with a normal distribution and mean annual rates set at 0.0, 0.05, and 0.1. The SD in migration rate was set at one-half of the mean. The only data available from the long-term study population in the Serengeti National Park (42) record an adult and adolescent immigration rate of 0.07 of the total population per year between 1991 and 2011 with an SD of 0.039 (Table S1).

Additional details on the methods are provided in *SI Materials and Methods* and the R code for the model is provided in Datasets S1–S3.

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