REVIEW

A strategic road map for conserving the Endangered dhole *Cuon alpinus* in India

Arjun SRIVATHSA* *School of Natural Resources and Environment, University of Florida, Gainesville 32611, USA, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville 32611, USA, Wildlife Conservation Society–India, 551, 7th Main Road Rajiv Gandhi Nagar, 2nd Phase, Kodigehalli, Bengaluru 560097, India, and National Centre for Biological Sciences, TIFR, GKVK campus, Bengaluru, India 560097. Email: asrivathsa@ufl.edu*

Sushma SHARMA *Wildlife Conservation Society–India, 7th Main Road Rajiv Gandhi Nagar, 2nd Phase, Kodigehalli, Bengaluru 560097, India. Email: sushmasharma@wcsindia.org*

Priya SINGH *National Centre for Biological Sciences, TIFR, GKVK campus, Bengaluru 560097, India. Email: karnisar@gmail.com*

Girish A. PUNJABI *Wildlife Conservation Trust, 11th floor, Mafatlal Centre, Nariman Point, Mumbai 400021, India. Email: girisharjunpunjabi@gmail.com*

Madan K. OLI *School of Natural Resources and Environment, University of Florida, Gainesville 32611, USA and Department of Wildlife Ecology and Conservation, University of Florida, Gainesville 32611, USA. Email: olim@ufl.edu*

*Correspondence author

Running title: A road map for dhole conservation in India

ABSTRACT

1. Large carnivores face high extinction risks, often exacerbated by the absence of adequate information on their ecological requirements, and the high economic and socio-political commitments that their conservation warrants. Country-scale conservation plans can serve as effective frameworks to prioritise areas, actions, and conservation investments.
2. We explore conservation tenets of retention, recovery and restoration for the Endangered dhole *Cuon alpinus* in India – a global stronghold for the species. Specifically, we: (1) examine the current status of dholes in India's states using a recent distribution assessment; (2) identify areas for directing management interventions – zones to be targeted for population recovery and for habitat recovery; (3) identify potential areas for range expansion;

(4) use eco-socio-political criteria to determine state-wise conservation priority scores and likelihood of conservation action; and (5) conduct an exhaustive review of all published literature on dholes.

3. Dholes occupy ~49% of potential habitats in 685 of mainland India's 2342 sub-districts. We identified 143 sub-districts with potential for dhole population recovery, 145 for habitat recovery, and 404 for range expansion. Of the 34 mainland states/union territories, 17 were identified as high priority for dhole conservation. Of these, nine are adequately equipped to implement management actions to conserve dholes, while eight need to improve capacity towards increasing likelihood of conservation success.
4. Literature on dholes (from 1874 to 2019; n=237) was dominated by natural history notes, followed by distribution records and studies of population ecology. A majority of the reviewed studies were from India (55% of 215 country-specific papers). The number of studies showed an exponential increase over time: 43% were published in the last decade.
5. Our review of published literature revealed significant knowledge gaps in terms of quantitative ecological assessments in dhole range-countries. Given this context, our results provide a comprehensive, multi-dimensional, and administratively feasible road map for dhole conservation in India, with potential applicability in other dhole range-countries and also for other threatened species.

Keywords: carnivores, conservation funding, India, policy, prioritisation, range expansion, species recovery

Received: 18 March 2020

Accepted: 28 April 2020

Editor: DR

INTRODUCTION

The past decade characterises an era of extensive documentation on global species extinctions (Szabo et al. 2012, Dirzo et al. 2014, Pimm et al. 2014). Large terrestrial mammal species, owing to their body sizes, geographic range limits and large home ranges, are often more susceptible to extinction risks than other taxonomic groups (Ceballos et al. 2005, 2017, Macdonald 2019). The conservation status of many obligate carnivore species is further exacerbated by their negative interactions with humans (Treves & Karanth 2003, Ripple et al. 2014). Large carnivores occupy an important trophic niche and play a crucial ecological role in regulating biotic community structure and dynamics (Ford & Goheen 2015). Therefore, range contractions and local extinctions of species in this guild, as evinced in recent times, can have critical trophic consequences across ecological systems and landscapes (Elmhagen et al. 2010, Estes et al. 2011, Wolf & Ripple 2017). These aspects may justify the enormous monetary, human-power and other resources invested in studying and conserving large carnivores (Brodie 2009, Smith et al. 2012).

The field of conservation biology has long been focused on species with small and declining populations (Caughley 1994, Bertolino 2017), typified by the current status of most large carnivores. The core tenets of conservation biology are thus centred around maintaining or increasing population sizes and ensuring the viability of small or declining populations (Soulé 1987). Within the constraints of ecologically imposed thresholds, Huggett (2005) postulates that retention, recovery and restoration may broadly be viewed as pivotal actions for conserving these populations. In the conservation context, this translates to: (1) retention – maintaining extant populations; (2) recovery – consolidating habitats and/or increasing population size; and (3) restoration – facilitating range expansion, recolonisation of putative historic range areas, and connectivity between populations, thus ensuring long-term ecological, demographic, and genetic viability. As a matter of course, these actions need to be coupled with assessment and reduction of anthropogenic and non-anthropogenic limiting factors, in tandem with continuous monitoring of population status and threats (Williams et al. 2002, Burgess et al. 2019).

Countries in the global south, and those in Asia in particular, harbour species that face greater threats compared to elsewhere in the world. This is primarily due to the cumulative effects of direct exploitation and changes in land-cover or habitats (Schipper et al. 2008, Godet & Devictor 2018, Davis & Glikman 2020). Country-specific species conservation plans can serve as effective frameworks for prioritising areas and actions for channelling conservation investments. Designing such plans requires several steps: first, the global context and relative importance of the focal range-country must be recognised, so as to identify realistic and logistically feasible conservation actions. Second, ecological knowledge of the species' distribution patterns, population sizes and threats need to be complemented with information on socio-economic and political attributes (O'Connor et al. 2003, Redpath et al. 2013). Third, spatial scale(s) and resolution(s) need be chosen such that priorities and actions can be most effective (Game et al. 2013). Finally, implementing conservation actions relies heavily on political will, performance and monetary investments, which determine administrative capacity and limitations (Dickman et al. 2015). Considered together, all these aspects synergistically contribute towards successful conservation outcomes.

Here, we focus on the Endangered Asiatic wild dog or dhole *Cuon alpinus* (Kamler et al. 2015), and present ecologically and socio-politically informed strategies for retention, recovery, restoration, and thereby, conservation of populations, closely linked to administration and policy in India. Our specific objectives were to: (1) examine current status of dholes in each state, based on a recent distribution assessment that incorporated ecological, biogeographic and anthropogenic factors; (2) identify sites (administrative sub-districts) for targeting interventions, i.e., areas where populations may need to be recovered, and areas warranting expansion of habitats; (3) gauge the potential for range expansion in areas beyond current dhole distribution limits; (4) evaluate state-wise dhole conservation priority score versus conservation likelihood score using ecological, social and political criteria, based on open data-sources and government records; and (5) provide an analysis of the current state of knowledge through a review of all published literature on dholes, identify research gaps and suggest future directions.

METHODS

Study species

Dholes are among the most threatened large carnivores in the world. The social, pack-living wild canids are found in 11 countries in south and southeast Asia; India harbours the largest population (Kamler et al. 2015). Some estimates suggest that dholes have undergone drastic range contractions of about 82% from their historic geographic range, and have a current global population of around 1000–2000 adult, mature individuals (Kamler et al. 2015, Wolf & Ripple 2017). Within India alone, dholes have lost ~60% of their former range in the last century (Karanth et al. 2010), showing persistent patterns of local extinctions (Srivathsa et al. 2019a). Historically widespread in the country, dholes were treated as ‘vermin’ and bounty-hunted through most of the 20th century (Kamler et al. 2015). Dholes now persist in small, presumably declining populations, mostly restricted to forest habitats (Sillero-Zubiri et al. 2004, Karanth et al. 2009, Punjabi et al. 2017, Srivathsa et al. 2019a, b); production agroforests abutting forested

Protected Areas provide secondary habitats for the species (Kumara et al. 2004, Srivathsa et al. 2014, Gangadharan et al. 2016). Dholes are sensitive to anthropogenic disturbance; studies show strong negative associations between dholes and domestic cattle abundance or activity in forested areas at multiple spatial scales (Srivathsa et al. 2014, Punjabi et al. 2017, Srivathsa et al. 2019a, b, 2020a). Most dhole metapopulations in India are clustered in three landscapes: the Western Ghats, Central India and Northeast India (Fig. 1). These metapopulations are generally structured such that source populations occur within Protected Areas and the surrounding unprotected forest–agroforest matrix perhaps serves as sinks (see Srivathsa et al. 2014, Punjabi et al. 2017, Srivathsa et al.2019a, 2020a).

Current status in Indian states

We used the countrywide sub-district level probabilities of dhole occupancy (Srivathsa et al. 2020a) as a basis to gauge the current status of their populations in India's states and Union Territories (collectively referred to as 'states'). Spatial patterns of dhole distribution based on the occupancy probabilities are shown in Fig. 1. Using these probabilities, we generated four metrics for each state: (1) percentage of area occupied by dholes within the extent of their key habitats, i.e. forests and agroforests, in the state; (2) dhole-occupied area in the state as a percentage of total area occupied throughout India; (3) number of Protected Areas with potential source populations – these are wildlife reserves where estimated occupancy was greater than the median occupancy probability in the country; and (4) percentage of dhole-occupied areas under protection as National Parks or Wildlife Sanctuaries. Given that there are no quantitative estimates of dhole abundance based on robust statistical methods for any part of their range, we assumed that the four metrics together (summed as 'status score' for each state) would serve as reasonable surrogates, indicative of their population status and the relative importance of each state for dholes.

Potential areas for recovery

We recognise two key actions for dhole conservation that necessitate proactive management interventions: (1) population recovery (PR) in sub-districts where dholes currently subsist at sub-optimal numbers despite the availability of adequate habitat; and (2) habitat recovery (HR) in sub-districts where populations may be faring well but the extent of suitable habitat is relatively small or restricted. Again, because true population estimates for dholes are not available, we use spatial probabilities of occupancy as a proxy for dhole abundance (the two are potentially correlated at larger spatial scales; see Guisan et al. 2013). We identified sub-districts that qualify for PR and HR using the following approach. First, we generated a correlative scatter plot with sub-district-level occupancy probabilities against forest cover (km^2) in each sub-district (Appendix S1). We parsed the data into four subsets based on median values of occupancy probability and forest cover extent. Here, we were interested in two subsets: PR sub-districts, where local occupancy was lower than the overall median occupancy (countrywide) but the associated forest cover extent was higher than the overall median value of forest cover (countrywide, within dhole range); and HR sub-districts, where local occupancy was higher than the overall median occupancy but local forest cover was lower than the overall median value of forest cover (Appendix S1). We then assigned priority scores to PR sub-districts based on decreasing order of occupancy probabilities, i.e. areas where occupancy was furthest from the median received the lowest scores. Similarly, scores for HR sub-districts were assigned based on decreasing order of forest cover extent, i.e. areas with lower forest cover were assigned lower scores. Our rationale was that sub-districts with PR or HR values closer to the median would require relatively lower management efforts to achieve a net gain in population or habitat recovery, and therefore should receive higher priority for dhole conservation efforts.

Potential areas for range expansion

The literature on restoration of terrestrial mammals (or rewilding) is riddled with myriad combinations of ecological, geographic, phylogenetic and taxonomic considerations for determining focal areas and actions (e.g., Svenning et al. 2016, Monsarrat et al. 2019). Although it would be desirable to have dholes recolonise all areas within their historical range, loss of habitat, persistent changes in land use, decline in prey populations, increasing human populations and associated impacts, and the population or distribution dynamics of the species itself, limit the locations and extent where range expansion is realistically plausible. Given this background, we identified potential areas at the sub-district level for dhole range expansion in India through a stepwise approach. First, we selected sub-districts that: (1) had at least 100 km^2 forest cover, assuming this would be a minimum threshold for at least one pack of dholes to become established (see Srivathsa et al. 2017); and (2) were within 300 km of any of the Protected Areas with source populations. While there is no documented evidence of long-distance dispersal by dholes, we assumed 300 km to be a reasonable upper limit, considering the species' body size, home range size and ecological constraints (Bowman et al. 2002, Santini et al. 2013, Whitmee & Orme 2013). We then removed sub-districts that were not contiguous with current dhole range, since these areas, even if they were recolonised, are unlikely to sustain viable populations in the long term. Next, we ranked the remaining sub-districts based on five criteria: habitat extent (forests and agroforests; km^2), extent of Protected Areas, Euclidean distance to nearest Protected Area with source populations, projected human population density for the year 2020, and density of cattle (data descriptions and sources are in Appendix S2). Values for the latter three were converted to inverse-form to account for a negative effect. We then standardised the individual criteria (z-transformation) and summed across the five categories to arrive at a final range expansion potential score for each sub-district; a larger value thus indicated higher potential for dhole range expansion.

State-wise priority and likelihood of conservation action

To calculate a dhole conservation priority score for each state, we included: (1) the status score, as explained above under 'Current status in Indian states'; (2) state-wise recovery potential score, calculated as a sum of PR and HR scores, along with inverse-transformed values for projected human population density for 2020 and density of cattle (as constraints for sub-districts within current dhole range) and (3) state-wise range expansion potential score, calculated as the sum of sub-district-wise values outside current dhole-range, as described in the previous section. The final dhole conservation priority score for each state was the weighted sum of z-transformed values of these three scores ('conservation priority score' and 'combined weighted priority score' henceforth used interchangeably). We weighted the three metrics such that current status was twice as important as recovery potential, which in turn was twice as important as range expansion potential (i.e. the scores were weighted as 1, 0.5 and 0.25). We did so positing that maintaining the current status of dhole populations should take precedence over any additional recovery efforts; using the same rationale, range expansion would be the most ambitious criterion, and therefore, of lower priority than the former two. All metrics described above are presented in Appendix S3.

Gauging the likelihood of conservation action can be complex, and this likelihood is difficult to quantify. We used a set of metrics (see Dickman et al. 2015) that we believed would be conducive to approximate state-level capacity to undertake conservation efforts.

(1) Gross Domestic Product (GDP) – we assumed that a state's economic status is closely linked to its administrative efficacy in implementing conservation action. We used GDP (%) for each state, averaged over annual values from 2015 to 2018, as an indicator for economic status.
(2) Poverty – corollary to the GDP, poverty levels can be indicative of locations where states ought to prioritise and invest in infrastructure development, economic growth and human welfare. We used average poverty headcount (% of total population) for each state from government census records. Values were inverse-transformed to account for a negative effect.
(3) State budget for forest and wildlife sectors – the states' average budgetary spending in forest and wildlife sectors from 2015 to 2018, calculated as average percentage of annual state budgets.
(4) Federal budget – besides state-level budgets, states receive additional federal funds for management of Tiger Reserves; these reserves represent a substantial proportion of PAs with dhole source populations. We included federal support sanctioned to individual states' Tiger Reserves, calculated as total funds received from 2015 to 2018.
(5) Infrastructure – rejection rate of forest clearance requests, measured as the percentage of infrastructure project proposals rejected (against all proposals approved/approved in principle/rejected; 2014–2019) by the states. We considered higher rejection rates to imply greater propensity of states to prioritise and value forest or wildlife conservation (data descriptions and details are in Appendix S2).
We calculated conservation likelihood scores as the sum of z-transformed values of the five metrics listed above. Finally, we compared state-wise conservation priority scores against the corresponding conservation likelihood scores to gauge their administrative capacity for effectively implementing dhole conservation efforts.

Current state of knowledge

Formulating science-based conservation plans for species can benefit from a detailed understanding of the current state of knowledge, identifying research gaps, and accordingly, determining future directions (e.g., Mori et al. 2018). We searched for peer-reviewed scientific articles, books, book chapters, natural history notes and grey literature through Google Scholar (www.scholar.google.com) and ISI Web of Science (www.webofknowledge.com) using keywords 'dhole', 'Asiatic wild dog' and '*Cuon alpinus*', without constraining the results to study location, region, country, or year. We reviewed references in field guides and books on natural history to locate older articles that may not have been digitally archived. We also used a snowball-sampling approach (Handcock & Gile 2011), using references within the located articles to find additional literature pertaining to dholes. We processed information from the literature thus obtained to examine global patterns in study locations, temporal trends in the number of studies, numbers of ex-situ and in-situ studies, and major thematic areas (viz., distribution/population ecology, descriptive natural history, behaviour/interactions, diet, human–dhole interactions/conservation/management, evolution/phylogeny/genetics, physiology/morphology, disease, and taxonomy/classification/description). Studies, articles or book chapters with only a passing mention of the species and providing little additional information were excluded from our review.

RESULTS

Dholes are currently found in 685 of 2342 sub-districts and 23 of 34 states in mainland India. They occupy around 249606 km^2 of forest and agroforest areas, which accounts for ~49% of potential habitats within their putative range. The distribution data we use were derived from the most recent country-wide assessment, which incorporated ecological, biogeographic and anthropogenic factors (prey species, habitat availability, extent of Protected Areas, rainfall, terrain ruggedness, cattle densities and human densities; see Srivathsa et al. 2020a). With respect to the current status of dholes, the states of Karnataka, Chhattisgarh, Arunachal Pradesh and Maharashtra ranked the highest (Table 1). We identified 143 sub-districts for PR and 145 sub-districts for HR (Fig. 2a). Assuming that cattle density and human population density are key limiting factors for PR and HR, respectively, we present these alongside the map with scores for PR and HR potential (Fig. 2b). Following the stepwise criteria described above, 404 sub-districts qualified with potential for range expansion (Fig. 2c). With respect to conservation priority scores at the state level, Arunachal Pradesh, Madhya Pradesh, Maharashtra and Karnataka had the highest ranks. State-level maps for current status, recovery potential score, range expansion potential score and combined weighted priority score are presented in Fig. 3. State-level conservation likelihood scores are listed in Table 2 and visually depicted in Fig. 3.

Conservation priority scores (including current status scores, recovery potential scores and range expansion potential scores) and conservation likelihood scores are in Table 3. We used a quadrant-based approach to evaluate state-wise dhole conservation priority scores versus conservation likelihood scores (*sensu* Dickman et al. 2015). Nine states with high conservation priority scores also had high conservation likelihood scores (Fig. 4, upper-right quadrant). Eight states that qualified as high priority had low conservation likelihood scores (Fig. 4, upper-left quadrant). Here, the state of Arunachal Pradesh had the highest overall conservation priority score, but scored much lower in terms of conservation likelihood score, suggesting that the state government here should increase its investment in conserving dholes substantially. Six states had relatively high conservation likelihood scores, but rank low for conservation priority score. Here, efforts to revive and conserve dhole populations, if implemented carefully, are likely to be most effective in the state of Tripura.

Our literature searches returned a total of 237 items pertaining to dholes published from 1874 to 2019, consisting of journal articles (90%), books/book chapters (3.3%), theses (3.3%) and reports (3.3%). A majority of the country-specific studies (55% of 215) were from India (Fig. 5). There was an exponential increase in the number of studies over time: articles published after 2010 accounted for 43% of all the studies reviewed. Almost all recent studies had overlapping themes, with distribution/population ecology being the most common, followed by natural history and behaviour/interaction assessments. Studies examining diseases, and those assessing taxonomy/classification had the least number of records (Fig. 5). In-situ assessments (87% of 188 studies) far outnumbered ex-situ assessments, and 62% of the 237 studies reviewed had the dhole as the focal species, while 12% were multi-species assessments, with dhole as one of the focal species. The full list of studies and associated details is in Appendix S4.

DISCUSSION

Recognising the importance of spatial scale in prioritising conservation and management, our study separately elucidates sub-district-level actions required and state-level capacity for and likelihood of conserving dholes in India. The approach we use also demonstrates the utility and potential of combining ecological information with open-source data and publicly available government records to formulate conservation plans for relatively under-studied yet imperilled species under a unified framework.

We found that the states of Maharashtra, Madhya Pradesh and Karnataka ranked an order of magnitude higher than the others in terms of conservation priority, and are also adequately equipped to maintain the status quo, consolidate forest habitats, and allow dhole populations to recover (by increasing prey densities and reducing pressures from forest-grazing cattle). On the other hand, Arunachal Pradesh, Chhattisgarh, Odisha, Telangana and Goa will need to increase financial investments while also reducing the ease of granting forest clearances for infrastructure projects (Fig. 4) if they are to conserve the species. Securing habitat corridors to allow colonisation through natural dispersal or by means of assisted migration (IUCN 2013) will be required to enable dhole range expansion beyond the current range. For instance, improving habitat conditions and prey densities in the Eastern Ghats would strengthen the link between the Western Ghats and Central Indian dhole metapopulations (see Fig. 1). Although this would be an ambitious and expensive undertaking, the approach is likely to enhance genetic fitness (e.g., Hagen et al. 2015), increase viability of extant sub-populations, and thereby benefit the overall dhole population in India – a global stronghold for the species.

Despite the academic debates on trade-offs between conserving species diversity versus conserving single species with declining populations (Arthur et al. 2004, Wilson et al. 2019), most management approaches still focus on single-species conservation. This is perhaps because actions focused on single species can be more clearly defined, and the outcomes may be measured in more tangible terms (Young et al. 2014, Burgess et al. 2019). Conserving a single large carnivore species could, however, have undesirable consequences for humans, protected prey species, or other protected co-predators (Marshall et al. 2016; Nattrass et al. 2020). Negative human–dhole interactions, arising largely due to livestock depredation, are prevalent mostly in the north-eastern states of India. This is potentially explained by low densities of large wild prey, high economic value of livestock, and a socio-cultural legacy of negative perceptions towards dholes in north-east India (Lyngdoh et al. 2014, Srivathsa et al. 2020b). Further, wildlife managers in parts of India generally believe that dholes negatively impact populations of the tiger *Panthera tigris* (a protected and politically important carnivore), and thereby view the dhole as a problem species. This notion has been challenged by recent studies that show how tigers and dholes can co-exist, provided there are adequate densities of medium-sized to large prey (Karanth et al. 2017). We assert that managers of individual Protected Areas and state Forest Departments should address these nuances while formulating management plans for dholes.

The literature pertaining to return-on-investment approaches in the conservation milieu is vast and prolific (e.g., Naidoo et al. 2006, Murdoch et al. 2007, 2010, Boyd et al. 2015). Returns are important considerations given the general scarcity of conservation funds and the wide mismatch between places where funding is required versus places where funds are channelled (see Larson et al. 2016). In our assessment, we used relative costs (cattle densities; see Srivathsa et al. 2019a, 2020a) rather than absolute costs representing efforts required to recover dhole populations. We used human population density to represent a range of land acquisition costs, opportunity costs, and transfer costs, among others (see Boyd et al. 2015). We did so because India is socio-economically hyperdiverse, with highly variable laws and policies, enforcement costs, landholding sizes, land-dependence levels, and land-purchase costs. These aspects may be explicated through local-scale assessments, where it would be more apposite to determine absolute values of returns on investments. We also note that our evaluation was limited to federal- and state-sponsored financial investments. We could not account for the role of non-governmental institutions that bring additional resources through research, conservation action, and litigation funding (Evans et al. 2019), which may marginally alter the dhole conservation capacity–likelihood relationship examined in this study.

A primary limitation of our assessment is that we rely on dhole distribution estimates as a surrogate for population sizes at the sub-district scale. Besides the dearth of statistically robust, quantitative studies about dhole population sizes, our review of dhole literature (1874–2019) also revealed persistent inadequacy of information on movement and dispersal ecology, precluding us from undertaking formal spatial prioritisation analyses that rely on target-based optimisations (*sensu* Moilanen 2014). Another caveat of our assessment is that information similar to what was used in this study is not available for Nepal, Bhutan, China and Myanmar – dhole range-countries that share borders with India. Our range expansion potential score, which includes data on the distance to the nearest source population, may need revisions for some areas in the northern and north-eastern states, when such information becomes available. These caveats provide opportunities for directing future research efforts. Along the same line, we found that a substantial proportion of studies we reviewed were either descriptive natural history notes or distribution (presence) records. In addition to the knowledge gaps mentioned above, dhole conservation would benefit from prioritising future work on examining ecological limits imposed by density dependence, potential and functional connectivity between populations in critical landscapes, long-term demographic effects of socially dominant competitors such as the tiger (see Steinmetz et al. 2013, Karanth et al. 2017), disease dynamics linked to population cycles, and negative interactions with free-ranging dogs (see Srivathsa et al. 2019b).

CONCLUSION

Dholes have benefited from conservation efforts aimed at the protection of tigers, due to the high degree of overlap in their geographic ranges (Goodrich et al. 2015, Kamler et al. 2015). Unfortunately, the tiger-centric conservation model currently practiced in India may not be optimal for dhole conservation in the long term (e.g., see Kumar et al. 2019), because it does not account for or address many dhole-specific threats and issues discussed in this study. India does not have a conservation plan tailored for dholes, nor does the species – to the best of our knowledge – have targeted management actions in any Protected Area's management plan. Dholes are legally protected under the provisions of Schedule II of India's Wild Life (Protection) Act; but this translates to reactive measures (in cases involving persecution or poaching), and not proactive actions. In light of these aspects, we strongly argue for greater scientific focus and conservation monitoring of the dhole – the only Endangered large carnivore in India besides the tiger (Goodrich et al. 2015, Kamler et al. 2015). The findings presented here may be used to create a strategic road map for dhole conservation in India, and also serve as a template for planning conservation and management of dhole populations in other range-countries. Furthermore, as systematic conservation planning for several threatened species in tropical countries is vitiated by similar levels of data-deficiency (Wilson et al. 2016), we believe our approach may be adapted and implemented as a preliminary step for formulating management frameworks for such species.

ACKNOWLEDGEMENTS

We are grateful to the University of Florida and Wildlife Conservation Society–India for providing institutional and logistical support. A.S. was supported by Wildlife Conservation Society's Christensen Conservation Leaders Scholarship, Wildlife Conservation Network's Sidney Byers Fellowship, and the University of Florida. G.A.P. was supported by IDEA Wild. The study was supported in part by funds from Liz Claiborne and Art Ortenberg Foundation and Wildlife Conservation Network. We thank members of the Wild Canids–India Project: I. Majgaonkar, M.M. Chawla and A. Banerjee for their contributions; K.U. Karanth, R.J. Fletcher, R.M. Dorazio and D.P. Onorato for useful discussions that led to shaping the ideas for the study;

M.A. Agnishikhe, A. Das, T. Kothawalla, D. Ganguly, K. Chauhan and A. Simon for their assistance in data compilation, processing and preliminary analysis.

REFERENCES

Arthur JL, Camm JD, Haight RG, Montgomery CA, Polasky S (2004) Weighing conservation objectives: maximum expected coverage versus endangered species protection. *Ecological Applications* 14: 1936–1945.

Bertolino S (2017) Distribution and status of the declining garden dormouse *Eliomys quercinus. Mammal Review* 47: 133–147.

Bowman J, Jaeger JA, Fahrig L (2002) Dispersal distance of mammals is proportional to home range size. *Ecology* 83: 2049–2055.

Boyd J, Epanchin-Niell R, Siikamäki J (2015) Conservation planning: a review of return on investment analysis. *Review of Environmental Economics and Policy* 9: 23–42.

Brodie JF (2009) Is research effort allocated efficiently for conservation? Felidae as a global case study. *Biodiversity and Conservation* 18: 2927–2939.

Burgess M, Gregory R, Wilson J, Gillings S, Evans A, Chisholm K et al. (2019) A new framework of spatial targeting for single-species conservation planning. *Landscape Ecology* 34: 2765–2778.

Caughley G (1994) Directions in conservation biology. *Journal of Animal Ecology* 63: 215–244.

Ceballos G, Ehrlich PR, Soberón J, Salazar I, Fay JP (2005) Global mammal conservation: what must we manage? *Science* 309: 603–607.

Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences* 114: 6089–6096.

Davis EO, Glikman JA (2020) An assessment of wildlife use by Northern Laos nationals. *Animals* 10: 685.

Dickman AJ, Hinks AE, Macdonald EA, Burnham D, Macdonald DW (2015) Priorities for global felid conservation. *Conservation Biology* 29: 854–864.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B (2014) Defaunation in the Anthropocene. *Science* 345: 401–406.

Elmhagen B, Ludwig G, Rushton SP, Helle P, Lindén H (2010) Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* 79: 785–794.

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ et al. (2011) Trophic downgrading of planet Earth. *Science* 333: 301–306.

Evans MJ, Malcom JW, Li YW (2019) Novel data show expert wildlife agencies are important to Endangered species protection. *Nature Communications* 10: 1–9.

Ford AT, Goheen JR (2015) Trophic cascades by large carnivores: a case for strong inference and mechanism. *Trends in Ecology & Evolution* 30: 725–735.

Game ET, Kareiva P, Possingham HP (2013) Six common mistakes in conservation priority setting. *Conservation Biology* 27: 480–485.

Gangadharan A, Vaidyanathan S, St. Clair CC (2016) Categorizing species by niche characteristics can clarify conservation planning in rapidly-developing landscapes. *Animal Conservation* 19: 451–461.

Godet L, Devictor V (2018) What conservation does. *Trends in Ecology & Evolution* 33: 720–730.

Goodrich J, Lynam A, Miquelle D, Wibisono H, Kawanishi K, Pattanavibool A et al. (2015) *Panthera tigris*. The IUCN Red List of Threatened Species 2015: e.T15955A50659951.

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI et al. (2013) Predicting species distributions for conservation decisions. *Ecology Letters* 16: 1424–1435.

Hagen SB, Kopatz A, Aspi J, Kojola I, Eiken HG (2015) Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. *Proceedings of the Royal Society B: Biological Sciences* 282: 20150092.

Handcock MS, Gile KJ (2011) Comment: on the concept of snowball sampling. *Sociological Methodology* 41: 367–371.

Huggett AJ (2005) The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation* 124: 301–310.

IUCN Species Survival Commission (2013). Guidelines for reintroductions and other conservation translocations, version 1.0. *Gland, Switzerland: International Union for Conservation of Nature.*

Kamler JF, Songsasen N, Jenks K, Srivathsa A, Sheng L, Kunkel K (2015) *Cuon alpinus*. The IUCN Red List of Threatened Species 2015: e. T5953A72477893.

Karanth KK, Nichols JD, Karanth KU, Hines JE, Christensen NL (2010) The shrinking ark: patterns of large mammal extinctions in India. *Proceedings of the Royal Society B: Biological Sciences* 277: 1971–1979.

Karanth KU, Srivathsa A, Vasudev D, Puri M, Parameshwaran R, Kumar NS (2017) Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences* 284: 20161860.

Kumara HN, Kumar MA, Sharma AK, Sushma HS, Singh M, Singh M (2004) Diversity and management of wild mammals in tea gardens in the rainforest regions of the Western Ghats, India: a case study from a tea estate in the Anaimalai Hills. *Current Science* 87: 1282–1286.

Kumar U, Awasthi N, Qureshi Q, Jhala Y (2019) Do conservation strategies that increase tiger populations have consequences for other wild carnivores like leopards? *Scientific Reports* 9: 1–8.

Larson ER, Howell S, Kareiva P, Armsworth PR (2016) Constraints of philanthropy on determining the distribution of biodiversity conservation funding. *Conservation Biology* 30: 206–215.

Lyngdoh S, Gopi GV, Selvan KM, Habib B (2014) Effect of interactions among ethnic communities, livestock and wild dogs (*Cuon alpinus*) in Arunachal Pradesh, India. *European Journal of Wildlife Research* 60: 771–780.

Macdonald DW (2019) Mammal conservation: old problems, new perspectives, transdisciplinarity, and the coming of age of conservation geopolitics. *Annual Review of Environment and Resources* 44: 61–88.

Marshall KN, Stier AC, Samhouri JF, Kelly RP, Ward EJ (2016). Conservation challenges of predator recovery. *Conservation Letters* 9: 70–78.

Moilanen A, Pouzols FM, Meller L, Veach V, Arponen A, Leppänen J, Kujala H (2014) *Zonation—spatial conservation planning methods and software. Version 4.* Helsingin Yliopisto, Helsinki.

Monsarrat S, Jarvie S, Svenning JC (2019) Anthropocene refugia: integrating history and predictive modelling to assess the space available for biodiversity in a human-dominated world. *Philosophical Transactions of the Royal Society B* 374: 20190219.

Mori E, Zozzoli R, Menchetti M (2018) Global distribution and status of introduced Siberian chipmunks *Eutamias sibiricus*. *Mammal Review* 48: 139–152.

Murdoch W, Polasky S, Wilson KA, Possingham HP, Kareiva P, Shaw R (2007) Maximizing return on investment in conservation. *Biological Conservation* 139: 375–388.

Murdoch W, Ranganathan J, Polasky S, Regetz J (2010) Using return on investment to maximize conservation effectiveness in Argentine grasslands. *Proceedings of the National Academy of Sciences* 107: 20855–20862.

Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M (2006) Integrating economic costs into conservation planning. *Trends in Ecology & Evolution* 21: 681–687.

Nattrass N, Drouilly M, O'Riain MJ (2020) Learning from science and history about black-backed jackals *Canis mesomelas* and their conflict with sheep farmers in South Africa. *Mammal Review* 50:101–111.

O'Connor C, Marvier M, Kareiva P (2003) Biological vs. social, economic and political priority-setting in conservation. *Ecology Letters* 6: 706–711.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN et al. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344: 1246752.

Punjabi GA, Edgaonkar A, Srivathsa A, Ashtaputre S, Rao MK (2017) Distribution of the dhole in its northern range limits in the Western Ghats, India. *Canid Biology & Conservation* 20: 7–13.

Redpath SM, Young J, Evely A, Adams WM, Sutherland WJ, Whitehouse A et al. (2013) Understanding and managing conservation conflicts. *Trends in Ecology & Evolution* 28: 100–109.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M et al. (2014) Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484.

Santini L, Di Marco M, Visconti P, Baisero D, Boitani L, Rondinini C (2013) Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix* 24: 181–186.

Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V et al. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322: 225–230.

Sillero-Zubiri C, Hoffmann M, Macdonald DW (2004) *Canids: Foxes, Wolves, Jackals, and Dogs: Status Survey and Conservation Action Plan*. IUCN/SSC Canid Specialist Group. Gland, Switzerland and Cambridge, UK.

Smith RJ, Veríssimo D, Isaac NJ, Jones KE (2012) Identifying Cinderella species: uncovering mammals with conservation flagship appeal. *Conservation Letters* 5: 205–212.

Soulé ME (1987) *Viable Populations for Conservation.* Cambridge University Press, Cambridge, UK.

Srivathsa A, Karanth KK, Jathanna D, Kumar NS, Karanth KU (2014) On a dhole trail: examining ecological and anthropogenic correlates of dhole habitat occupancy in the Western Ghats of India. *PloS One* 9: e98803.

Srivathsa A, Kumar NS, Karanth KU (2017) Home range size of the dhole estimated from camera-trap surveys. *Canid Biology & Conservation* 20: 1–4.

Srivathsa A, Karanth KU, Kumar NS, Oli MK (2019a) Insights from distribution dynamics inform strategies to conserve a dhole *Cuon alpinus* metapopulation in India. *Scientific Reports* 9: 3081.

Srivathsa A, Puri M, Karanth KK, Patel I, Kumar NS (2019b) Examining human–carnivore interactions using a socio-ecological framework: sympatric wild canids in India as a case study. *Royal Society Open Science* 6: 182008.

Srivathsa A, Majgaonkar I, Sharma S, Punjabi GA, Singh P, Chawla MM, Banerjee A (2020a) Opportunities for prioritizing and expanding conservation enterprise in India using a guild of carnivores as flagships. *Environmental Research Letters* 15: 064009.

Srivathsa A, Sharma S, Oli MK (2020b) Every dog has its prey: rangewide assessment of links between diet patterns, livestock depredation, and human interactions for an Endangered carnivore. *Science of the Total Environment* 714: 136798.

Steinmetz R, Seuaturien N, Chutipong W (2013) Tigers, leopards, and dholes in a half-empty forest: assessing species interactions in a guild of threatened carnivores. *Biological Conservation* 163: 68–78.

Svenning JC, Pedersen PB, Donlan CJ, Ejrnæs R, Faurby S, Galetti M et al. (2016) Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences* 113: 898–906.

Szabo JK, Khwaja N, Garnett ST, Butchart SH (2012) Global patterns and drivers of avian extinctions at the species and subspecies level. *PloS One* 7(10): e47080.

Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491–1499.

Whitmee S, Orme CDL (2013) Predicting dispersal distance in mammals: a trait-based approach. *Journal of Animal Ecology* 82: 211–221.

Williams BK, Nichols JD, Conroy MJ (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego, California, USA.

Wilson KA, Auerbach NA, Sam K, Magini AG, Moss ASL, Langhans SD et al. (2016) Conservation research is not happening where it is most needed. *PLoS Biology* 14(3): e1002413.

Wilson S, Schuster R, Rodewald AD, Bennett JR, Smith AC, La Sorte FA et al. (2019) Prioritize diversity or declining species? Trade-offs and synergies in spatial planning for the conservation of migratory birds in the face of land cover change. *Biological Conservation* 239: 108285.

Wolf C, Ripple WJ (2017) Range contractions of the world's large carnivores. *Royal Society Open Science* 4: 170052.

Young RP, Hudson MA, Terry AMR, Jones CG, Lewis RE, Tatayah V et al. (2014) Accounting for conservation: using the IUCN Red List Index to evaluate the impact of a conservation organization. *Biological Conservation* 180: 84–96.

Table 1. State-wise information on dhole populations in India. Occupied area is calculated as the product of sub-district level occupancy probabilities with extent of habitat in the corresponding sub-district, summed for each state. Percentage occupied is the percentage of potential habitat within each state that is occupied by dholes; percentage in India is the dhole-occupied area in each state as a percentage of the total dhole-occupied area in India; percentage protected refers to the percentage of dhole-occupied areas that are included in National Parks or Wildlife Sanctuaries. Source population PAs are counts of Protected Areas where estimated dhole occupancy is higher than the median. S=state; UT=Union Territory.

Name of state	Category	Occupied area (km^2)	Percentage occupied	Percentage in India	Percentage protected	Source population PAs
Andhra Pradesh	S	11456	46.41	4.59	76.87	7
Arunachal Pradesh	S	34418	55.24	13.79	30.49	11
Assam	S	7593	25.87	3.04	64.95	2
Bihar	S	755	10.57	0.30	100.00	0
Chandigarh	UT	0	0.00	0.00	0.00	0
Chhattisgarh	S	32353	58.56	12.96	23.24	14
Dadra–Nagar Haveli	UT	0	0.00	0.00	0.00	0
Daman–Diu	UT	0	0.00	0.00	0.00	0
Goa	S	890	76.39	0.36	86.95	5
Gujarat	S	0	0.00	0.00	0.00	0
Haryana	S	0	0.00	0.00	0.00	0
Himachal Pradesh	S	0	0.00	0.00	0.00	0
Jammu Kashmir*	S	0	0.00	0.00	0.00	0
Jharkhand	S	9045	36.14	3.62	40.45	3
Karnataka	S	21406	55.57	8.58	46.15	21
Kerala	S	9623	66.95	3.86	29.59	20
Madhya Pradesh	S	25224	29.02	10.11	31.93	13
Maharashtra	S	21491	42.09	8.61	26.96	21
Manipur	S	4704	41.35	1.88	3.81	1
Meghalaya	S	4194	31.41	1.68	20.63	1
Mizoram	S	5011	52.18	2.01	12.94	6
Nagaland	S	3959	51.41	1.59	6.24	1
NCT of Delhi	UT	0	0.00	0.00	0.00	0
Odisha	S	29501	49.81	11.82	21.24	9
Puducherry	UT	0	0.00	0.00	0.00	0

Punjab	S	0	0.00	0.00	0.00	0
Rajasthan	S	0	0.00	0.00	0.00	0
Sikkim	S	994	33.20	0.40	100.00	1
Tamil Nadu	S	6917	36.33	2.77	77.22	11
Telangana	S	11399	57.30	4.57	65.57	6
Tripura	S	779	16.00	0.31	39.92	1
Uttar Pradesh	S	1475	11.55	0.59	100.00	0
Uttarakhand	S	4695	22.64	1.88	100.00	4
West Bengal	S	1725	7.93	0.69	65.09	4

*Jammu Kashmir was a state during the time of analysis; it is currently split into Union Territories

Table 2. State-wise information on attributes used for calculating conservation likelihood scores. Average GDP corresponds to the mean of annual values from 2015 to 2018. Average poverty (%) data were extracted from government census records at the district level and processed to arrive at state-level averages. FW Budget is the state's average budgetary spending in forest and wildlife sectors (expressed as a proportion of annual state budgets 2015–2018). Tiger Reserve (TR) funds are federal funds sanctioned to individual states' TRs, calculated as total funds received from 2015 to 2018. Forest Clearance (FC) rejection rate is the proportion of infrastructure project proposals rejected against all proposals (approved/approved in principle/rejected; 2014–2019). S=state; UT=Union Territory.

Name	**Category**	**Average GDP (%)**	**Average poverty (%)**	**FW budget (%)**	**TR funds (USD)**	**FC rejection rate (%)**
Andhra Pradesh	S	4.58	21.96	0.30	1,028,739	7.43
Arunachal Pradesh	S	0.13	29.38	0.84	2,271,146	0.00
Assam	S	1.67	42.26	1.00	7,829,764	0.00
Bihar	S	2.77	52.41	0.30	1,886,062	0.00
Chandigarh	UT	0.22	16.84	0.00	0	0.00
Chhattisgarh	S	1.67	36.46	1.10	3,493,415	2.78
Dadra–Nagar Haveli	UT	0.00	46.61	0.00	0	0.00
Daman–Diu	UT	0.00	23.52	0.00	0	0.00
Goa	S	0.41	6.73	0.13	0	0.00
Gujarat	S	7.59	25.64	0.60	0	0.00
Haryana	S	3.64	15.58	0.57	0	0.21
Himachal Pradesh	S	0.83	10.05	1.30	0	1.57
Jammu Kashmir*	S	0.83	8.04	1.27	0	0.00
Jharkhand	S	1.56	48.12	0.90	1,060,249	11.11
Karnataka	S	7.83	22.81	1.07	10,068,888	6.02
Kerala	S	4.12	10.79	0.57	2,706,334	11.11
Madhya Pradesh	S	4.16	46.90	1.83	38,176,486	0.00
Maharashtra	S	14.28	24.54	0.77	27,719,346	2.37
Manipur	S	0.14	46.61	1.37	0	0.00
Meghalaya	S	0.18	17.62	1.53	0	0.00
Mizoram	S	0.11	32.04	1.40	1,052,013	0.00
Nagaland	S	0.14	16.50	0.67	0	0.00
NCT of Delhi	UT	4.03	18.86	0.20	0	0.00
Odisha	S	2.51	49.98	0.83	4,576,708	2.91

Puducherry	UT	0.19	4.98	0.00	0	0.00
Punjab	S	2.82	13.04	0.17	0	0.54
Rajasthan	S	4.95	28.47	0.80	3,600,299	0.59
Sikkim	S	0.14	24.14	3.93	0	0.00
Tamil Nadu	S	8.57	25.17	0.40	8,135,968	4.00
Telangana	S	4.32	20.28	0.19	693,790	0.00
Tripura	S	0.26	8.25	1.10	0	14.29
Uttar Pradesh	S	8.19	41.96	0.33	3,733,829	0.00
Uttarakhand	S	1.29	18.92	1.80	4,289,302	1.44
West Bengal	S	5.80	32.73	0.47	2,254,074	0.00

* Jammu Kashmir was a state during the time of analysis; it is currently split into Union Territories

Table 3. State-wise (z-transformed) current status score, recovery potential score, range expansion potential score, conservation priority score (combined weighted priority score) and conservation likelihood scores. Details on calculations of these scores are presented in the Methods section. S=state; UT=Union Territory.

Name	Category	Current status score	Recovery potential score	Range expansion potential score	Conservation priority score	Conservation likelihood score
Andhra Pradesh	S	2.73	-0.36	2.29	3.12	0.69
Arunachal Pradesh	S	4.66	10.48	-2.86	9.18	-2.06
Assam	S	0.40	-0.37	1.37	0.56	-0.94
Bihar	S	-0.23	-1.38	-1.09	-1.19	-2.39
Chandigarh	UT	-3.52	-1.67	-2.86	-5.07	-2.81
Chhattisgarh	S	4.85	1.83	0.66	5.93	-0.52
Dadra–Nagar Haveli	UT	-3.52	-1.67	-1.37	-4.70	-3.80
Daman–Diu	UT	-3.52	-1.67	-2.86	-5.07	-3.29
Goa	S	2.91	-0.92	-2.86	1.74	-0.43
Gujarat	S	-3.52	-1.67	2.00	-3.86	-0.30
Haryana	S	-3.52	-1.67	-0.51	-4.49	-0.86
Himachal Pradesh	S	-3.37	-1.67	12.76	-1.01	0.47
Jammu Kashmir*	S	-3.52	-1.67	-2.86	-5.07	0.61
Jharkhand	S	0.44	0.25	-0.76	0.38	0.96
Karnataka	S	5.38	1.53	1.74	6.58	3.39
Kerala	S	4.09	0.09	-2.86	3.42	3.24
Madhya Pradesh	S	3.03	5.39	5.77	7.16	4.65
Maharashtra	S	4.30	3.66	3.42	6.98	6.09
Manipur	S	-1.10	0.33	7.28	0.88	-1.95
Meghalaya	S	-1.09	-0.52	-2.86	-2.07	-0.87
Mizoram	S	0.40	1.24	-2.86	0.31	-1.55
Nagaland	S	-0.69	-0.79	-2.86	-1.80	-1.93
NCT of Delhi	UT	-3.52	-1.67	-2.86	-5.07	-1.55
Odisha	S	3.39	1.45	-2.86	3.39	-0.62
Puducherry	UT	-3.52	-1.67	-2.86	-5.07	0.61
Punjab	S	-3.52	-1.67	-0.75	-4.55	-1.25
Rajasthan	S	-3.52	-1.67	2.52	-3.73	-0.31

Sikkim	S	0.89	0.28	-2.86	0.31	1.90
Tamil Nadu	S	2.50	0.45	2.06	3.24	1.85
Telangana	S	2.71	-0.49	-2.86	1.74	-1.48
Tripura	S	-1.52	-1.38	4.50	-1.08	3.99
Uttar Pradesh	S	-0.12	-1.18	0.13	-0.67	-0.37
Uttarakhand	S	1.27	-0.16	-2.86	0.48	0.65
West Bengal	S	-0.60	-1.06	0.92	-0.90	-0.93

*Jammu Kashmir was a state during the time of analysis; currently it is split into Union Territories

Figure legends

Fig. 1. Spatial probability of dhole occupancy mapped at the sub-district scale in India, adapted from Srivathsa et al. (2020a). Occupancy probabilities range from 0.03 to 0.96. Inset boxes are maps of landscapes where the three main dhole metapopulations occur, showing dhole habitats and source population Protected Areas (PAs): Western Ghats, Central India and Northeast India.

Fig. 2. (a) Sub-district-level scores for dhole population recovery 'PR' potential and habitat recovery 'HR' potential. Darker shades indicate higher scores. (b) Human population density and cattle density at the sub-district level, representing the key limiting factors for HR and PR potential, respectively. Darker shades indicate higher densities. (c) Sub-district level scores for dhole range expansion potential, beyond current dhole distribution limits. Darker shades indicate higher scores.

Fig. 3. State-level scores for current dhole status, potential for population/habitat recovery, potential for range expansion, combined weighted priority (or conservation priority), and conservation likelihood scores. Darker shades indicate higher values.

Fig. 4. Left panel: quadrant plot showing the relationship between state-wise dhole conservation priority scores and conservation likelihood scores. Vertical and horizontal lines represent corresponding median values. State codes: AP– Andhra Pradesh, AR– Arunachal Pradesh, AS– Assam, BH– Bihar, CG– Chhattisgarh, GA– Goa, GJ– Gujarat, HR– Haryana, HP– Himachal Pradesh, JK– Jammu Kashmir, JH– Jharkhand, KA– Karnataka, KL– Kerala, MP– Madhya Pradesh, MH– Maharashtra, MN– Manipur, ML– Meghalaya, MZ– Mizoram, NL– Nagaland, OR– Odisha, PB– Punjab, RJ– Rajasthan, SK– Sikkim, TN– Tamil Nadu, TS– Telangana, TR– Tripura, UP–Uttar Pradesh, UK– Uttarakhand, WB– West Bengal. Unnamed grey dots are Union Territories. Right panel: map of Indian states with colours representing the respective quadrant in which they appear in the left panel.

Fig. 5. Top left: country-wise numbers of studies pertaining to dholes (published from 1874 to 2019). Ex-situ studies conducted outside current or recent dhole range countries have been excluded from the map. Top right: temporal trends in dhole studies, shown as percentages of total studies (n=237) conducted every two decades. The last two decades are divided into 10-year intervals for ease of depiction. Bottom left: illustrative word cloud with major thematic areas in reviewed studies. Darker shades indicate themes that are repeated more often. Bottom right: percentage of ex-situ and in-situ studies (n=188).

SUPPORTING INFORMATION

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

Appendix S1. Dhole occupancy probabilities plotted against forest cover extent in the 2342 sub-districts in India. Black lines represent median values. Based on their position on the plot, sub-districts are identified as suitable targets for population recovery (PR) or habitat recovery (HR). In PR sub-districts, local occupancy was lower than the overall median occupancy but the associated forest cover extent was higher than the overall median value of forest cover (countrywide, within dhole range); in HR sub-districts, local occupancy was higher than the overall median occupancy but local forest cover was lower than the overall median.

Appendix S2. Data category descriptions and sources.

Appendix S3. State-wise scores for current status, recovery potential and range expansion potential.

Appendix S4. Full list of literature (n=237) reviewed for this study.

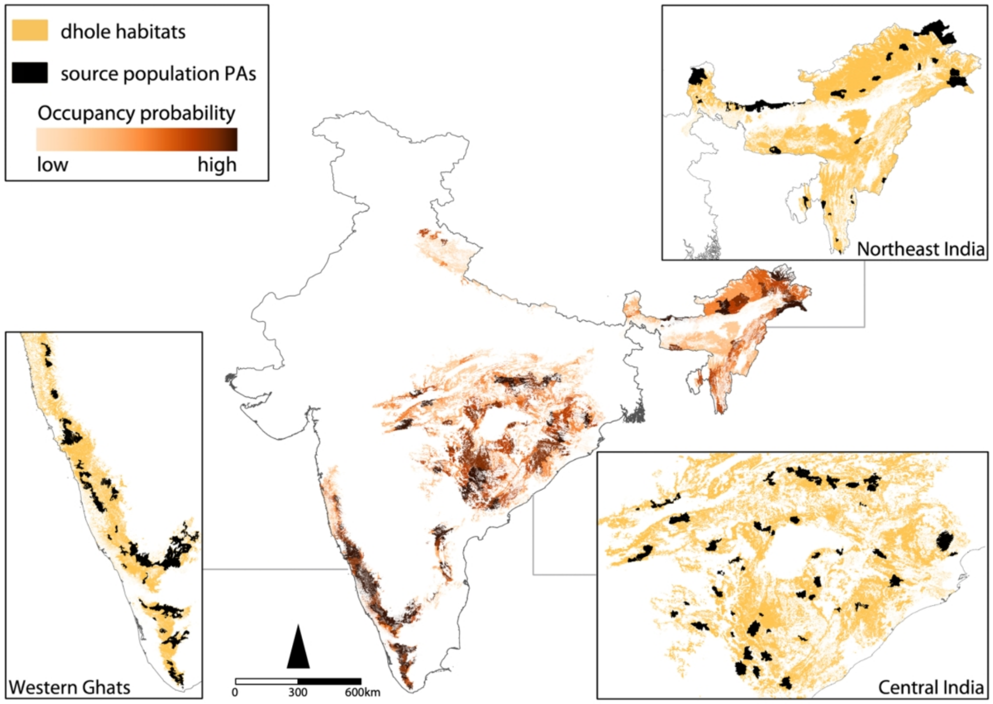

Figure 1. Spatial probability of dhole occupancy mapped at the sub-district scale in India, adapted from Srivathsa et al. (2020a). Occupancy probabilities range from 0.03 to 0.96. Inset boxes are maps of landscapes where the three main dhole metapopulations occur, showing dhole habitats and source population Protected Areas (PAs): Western Ghats, Central India and Northeast India.

211x149mm (300 x 300 DPI)

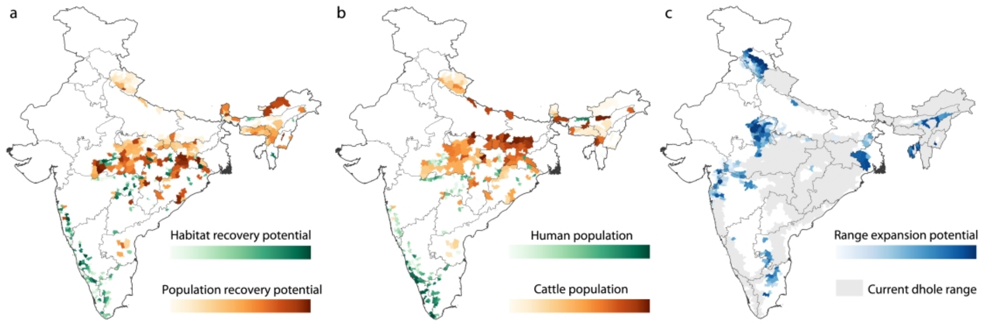

Figure 2. (a) Sub-district-level scores for dhole population recovery 'PR' potential and habitat recovery 'HR' potential. Darker shades indicate higher scores. (b) Human population density and cattle density at the sub-district level, representing the key limiting factors for HR and PR potential, respectively. Darker shades indicate higher densities. (c) Sub-district level scores for dhole range expansion potential, beyond current dhole distribution limits. Darker shades indicate higher scores.

423x140mm (300 x 300 DPI)

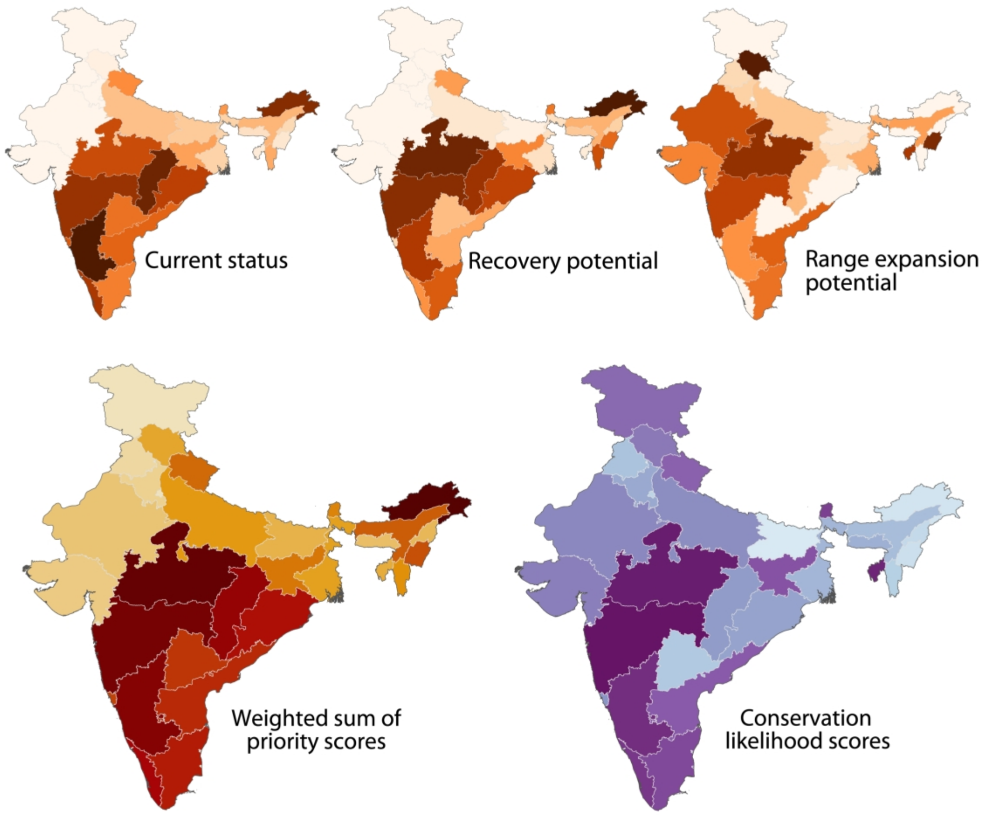

Figure 3. State-level scores for current dhole status, potential for population/habitat recovery, potential for range expansion, combined weighted priority (or conservation priority), and conservation likelihood scores. Darker shades indicate higher values.

254x216mm (300 x 300 DPI)

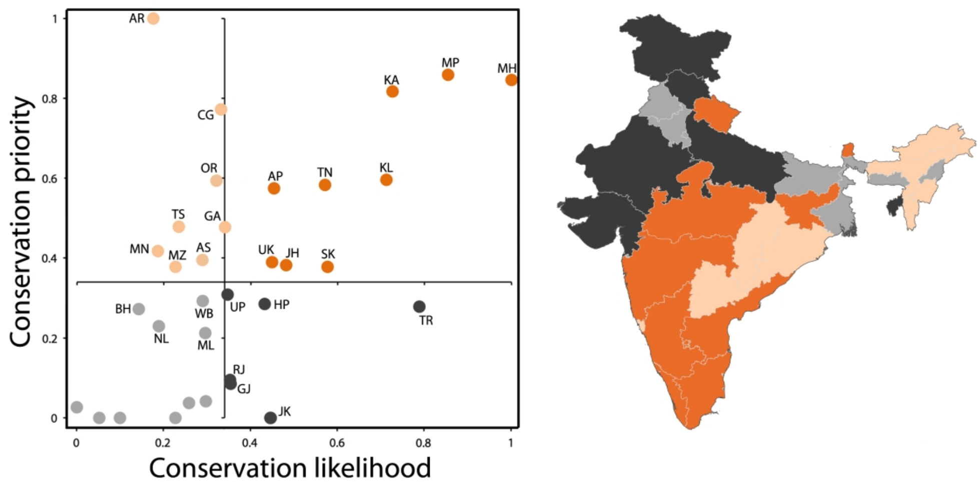

Figure 4. Left panel: quadrant plot showing the relationship between state-wise dhole conservation priority scores and conservation likelihood scores. Vertical and horizontal lines represent corresponding median values. State codes: AP– Andhra Pradesh, AR– Arunachal Pradesh, AS– Assam, BH– Bihar, CG– Chhattisgarh, GA– Goa, GJ– Gujarat, HR– Haryana, HP– Himachal Pradesh, JK– Jammu Kashmir, JH– Jharkhand, KA– Karnataka, KL– Kerala, MP– Madhya Pradesh, MH– Maharashtra, MN– Manipur, ML– Meghalaya, MZ– Mizoram, NL– Nagaland, OR– Odisha, PB– Punjab, RJ– Rajasthan, SK– Sikkim, TN– Tamil Nadu, TS– Telangana, TR– Tripura, UP–Uttar Pradesh, UK– Uttarakhand, WB– West Bengal. Unnamed grey dots are Union Territories. Right panel: map of Indian states with colours representing the respective quadrant in which they appear in the left panel.

254x134mm (300 x 300 DPI)

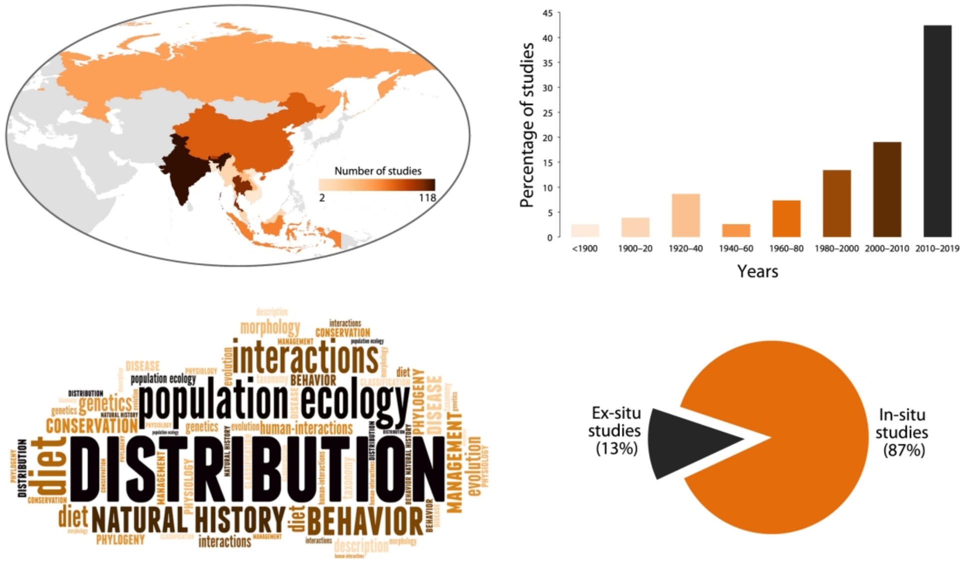

Figure 5. Top left: country-wise numbers of studies pertaining to dholes (published from 1874 to 2019). Ex-situ studies conducted outside current or recent dhole range countries have been excluded from the map. Top right: temporal trends in dhole studies, shown as percentages of total studies (n=237) conducted every two decades. The last two decades are divided into 10-year intervals for ease of depiction. Bottom left: illustrative word cloud with major thematic areas in reviewed studies. Darker shades indicate themes that are repeated more often. Bottom right: percentage of ex-situ and in-situ studies (n=188).

254x155mm (300 x 300 DPI)