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LETTER

Spatial ecology of cheetahs in India: Complexities beyond extrapolation from Africa

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Reintroduction is a well-established technique to restore species or populations to places from which they disappeared and ultimately to rebuild lost pathways for ecosystem functioning (IUCN/SSC, 2013). India's Project Cheetah was tasked to restore the cheetah in parts of its historical distribution range (Jhala, Ranjitsinh, et al., 2021) and has received widespread public and political support while also sparking scientific debate (Gopalaswamy et al., 2022; Tordiffe et al., 2023). One challenge is the need for baseline information on cheetah ecology in India due to the extinction of the species in the mid-20th century.

Wachter et al. (2023) provide a series of carefully formulated predictions on the potential space use of cheetahs in India's Kuno National Park (KNP) based on their perspective from a detailed understanding of cheetah spatial ecology in Namibia (e.g., Melzheimer et al., 2018, 2020). While we appreciate these insights, we address some contextual challenges that could affect the space use assumption on which their predictions build, we caution on the limitations of extrapolation, and discuss some of the management strategies that address the ranging patterns of released cheetahs in India.

In stating that male territories are separated by 20–23 km, Wachter et al. (2023) base their predictions of cheetah movements in India on data they collected primarily in the Namibian Kalahari savannah and on interpreting data from the Serengeti (Caro, 1994). Both ecosystems are distinct from KNP and while these two African systems have some differences, they comprise predominantly open vegetation, are relatively flat, with few and localized natural or anthropogenic barriers, and some of the world's lowest human population densities. In contrast, KNP is a more densely vegetated landscape with large watercourses some of which may be barriers to cheetah movement. Anthropogenic activity and domestic dogs in/near villages surrounding the park are likely strong deterrents through visual, audible, and physical disturbance. Differences in cheetah space use tactics are therefore foreseen and will likely affect all Wachter et al. (2023)'s predictions except perhaps Prediction 4.

As Wachter et al. (2023) mention in Prediction 3, individual cheetahs are expected to test the permeability of barriers and make large exploratory movements, particularly in the early stages of post-release (Walker et al., 2022). Such exploratory movements can connect established populations in the future but have the potential to cause conflict. To tackle such challenges, Project Cheetah has rapid response teams tasked with actively deterring cheetahs from risky areas. Reaction times are facilitated by intensive monitoring using GPS radiocollars with satellite communication technology. The reactive approaches of deterrence or if necessary, capture and movement of cheetahs back to the KNP complement proactive measures, including information and awareness campaigns with local communities in the pre-release phase and a compensation scheme traditionally used for livestock losses in India. These measures further increase tolerance levels towards cheetahs. They are likely to extend the landscape of coexistence (sensu Oriol-Cotterill et al., 2015) outside KNP boundaries into the broader ecosystem, as envisioned in the Cheetah Action Plan (Jhala, Ranjitsinh, et al., 2021), thereby alleviating some of the risk incurred in exploratory movements and territory establishment. However, not all eight cheetahs that Wachter et al. (2023) mentioned in their Prediction 3 made extensive exploratory movements during the monitoring period. In the first year of the project, of the 14 cheetahs that were released as free-ranging and monitored for ~800 days, most remained within the greater Kuno landscape and only two individuals had to be captured and brought back to the park for their safety. All cheetahs made kills of wild prey and there were only

two records of domestic animals being killed, which were promptly compensated. As of March 2024, no mortalities of the released cheetahs have occurred due to human-cheetah conflicts or by leopards (~20 leopards per 100 km^2). These initial observations are very encouraging and bode well for the establishment of the species within the greater Kuno landscape.

Cheetahs have complex territoriality mechanisms, as pointed out by Wachter et al. (2023) and documented in the literature (Marker et al., 2018; Melzheimer et al., 2018). Adult males may become territory holders to increase encounters with females and mating opportunities (Caro, 1994), hence the presence of female individuals may encourage site fidelity and home range characteristics of reintroduced males. The influence of female presence on male space use is currently being addressed as part of the release strategy at KNP. Preliminary data suggest that the spatial behavior of released male coalitions can be manipulated to revisit sites, using females temporarily kept in bomas inside the park located within the perceptual range of free-roaming males. In the absence of captive females, this strategy could potentially be mimicked by placing female scats periodically at conspicuous landmarks to emulate marking sites, but the efficacy of this approach has yet to be determined. The positive reinforcement of male cheetah movements using females as anchors complements the negative reinforcement described above for deterrence by the rapid response teams.

Wachter et al. (2023) state that cheetah densities are not usually greater than 1 individual/100 km^2. We agree that densities are generally low, but as described above, the environmental conditions in KNP differ from the study areas they reference. Moreover, historical densities could have been higher in productive cheetah habitats (Tordiffe et al., 2023). If only a few individuals are reintroduced, resulting low densities could lead to missed mating opportunities due to reduced encounters between males and females and potentially become a driver of population decline and conservation introduction failure (Deredec & Courchamp, 2007).

Cheetah distribution on the landscape and, ultimately, densities are the product of their movement decisions, which are determined by factors such as prey availability, hunting habitat configuration, perceived safety, competitive interactions, and the availability of noticeable features for territorial marking. Abundant resources may lead to relaxed territoriality and increased conspecific tolerance, as shown for other large felids (e.g., Elbroch et al., 2016; le Roex et al., 2022). Habitat productivity of KNP is arguably higher than in semiarid Namibian climates. Higher leopard densities in KNP (Jhala, Qureshi, & Yadav, 2021) and other parts of India relative to Namibia (Richmond-Coggan, 2019) also suggest such differences in productivity, although cheetah density in India could perhaps be limited by exploitative and interference competition from abundant leopard populations. Furthermore, even within Namibia's Central Kalahari, at least 60 adult and subadult cheetah individuals were detected across 4096 km^2. This suggests a robust population that might exceed 1/100 km^2 (Cheetah Conservation Fund, unpublished data), while densities of 1.94/100 km^2 were found in another Namibian biome (Fabiano et al., 2020). As pointed out recently in the literature, the spatially explicit capture-recapture method may not be best suited for cheetah population estimation (Edwards et al., 2018), yet few empirically derived density estimates are available for cheetah (Strampelli et al., 2022). All these complexities will potentially affect predictions of cheetah space use, and we argue that coming up with a robust set of predictions is challenging in the absence of historical baseline knowledge on cheetahs in India. Nonetheless, lack of data should not deter reintroduction, nor distract from learning valuable lessons along each step.

Overall, the predictions Wachter et al. (2023) laid out provide for an interesting debate but have limitations, as expected with any extrapolation process. Wachter et al. (2023)'s expectation that spacing among territory centers will be similar for cheetahs in India and Africa is disputable based on differences in a suite of factors, including vegetation, topography, prey availability, and human pressure. Scientific data on spatial ecology and territoriality tactics of cheetahs across environmental conditions are scant, and we caution against extrapolation among biomes and within and between continents. Data on cheetah spatial ecology from Indian release cheetahs will soon become available, providing valuable information regarding movement choices and the overall space use of those individuals. In the meantime, the releases into KNP were planned to be staggered, allowing lessons on behavior and spatial ecology in the novel environment to be learned and facilitating effective monitoring and adaptive decision-making. Although testing predictions can bring interesting insights, the adaptive management process will likely need to prioritize the well-being and success of the release animals over academic inquiry, in particular in the early stages of the project.

Ecological knowledge and project impact are expected to be enhanced with the expansion to additional suitable release sites, ultimately allowing the establishment of the species in India. In the initial years, human-mediated management will be required to connect the populations to function as a metapopulation. Once cheetah populations build up at the reintroduction sites, they are likely to disperse through the larger landscapes thereby

promoting a natural metapopulation structure. Reintroductions are tools to restore complex ecosystem functions, and conservation biologists need to use a combination of adaptive management options to make them successful. Though the insights on spatial ecology of cheetahs provided by Wachter et al. (2023) are useful, species ecological interactions are complex and often site-specific. Conservation and restoration projects, such as this historical reintroduction emerging from extensive planning and with high public and political support, need to be afforded time for fruition.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no data were analyzed.

B. Cristescu[1,2]
Y. V. Jhala[3]
B. Balli[1]
Q. Qureshi[3]
A. Schmidt-Küntzel[1]
A. S. W. Tordiffe[4]
V. van der Merwe[5]
S. Verschueren[1,6]
E. Walker[1]
L. Marker[1]

[1]*Cheetah Conservation Fund, Otjiwarongo, Namibia*
[2]*Namibia University of Science and Technology, Windhoek, Namibia*
[3]*Wildlife Institute of India, Dehradun, India*
[4]*University of Pretoria, Pretoria, South Africa*
[5]*The Metapopulation Initiative, Polokwane, South Africa*
[6]*University of Antwerp, Antwerp, Belgium*

Correspondence
B. Cristescu, Cheetah Conservation Fund, Otjiwarongo, Namibia.
Email: bogdan@cheetah.org

ORCID

B. Cristescu https://orcid.org/0000-0003-2964-5040
Y. V. Jhala https://orcid.org/0000-0003-3276-1384
A. Schmidt-Küntzel https://orcid.org/0000-0001-5108-2606
A. S. W. Tordiffe https://orcid.org/0000-0001-5416-3153
V. van der Merwe https://orcid.org/0000-0002-6637-588X
S. Verschueren https://orcid.org/0000-0003-1420-7689
E. Walker https://orcid.org/0000-0003-4946-7122
L. Marker https://orcid.org/0000-0002-1636-2191

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