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RESEARCH ARTICLE

Space use and survival of reintroduced Persian onagers

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Handling Editor: Jenny Macpherson**Abstract**

1. Reintroduction is a conservation priority aimed at restoring native species to parts of their historical range through the release of wild or captive-bred individuals. However, little is known about how reintroduced populations respond to habitat features and management interventions, such as the placement of ranger stations or the use of individuals from different origins.
2. We evaluated the reintroduction of the Critically Endangered Persian onager (*Equus hemionus onager*) in Kavir National Park, Iran, a desert ecosystem largely devoid of human disturbance. We conducted daily foot surveys (2022–2023) and collected demographic data from 2018 to 2024. Using Bayesian occupancy models and demographic analyses, we addressed two questions: (i) How is onager occupancy influenced by trade-offs between habitat characteristics and proximity to ranger stations? and (ii) to what extent do interventions, such as periodic restocking, affect survival and population growth over time?
3. Occupancy was positively associated with *Artemisia-Zygophyllum* shrub communities and proximity to ranger stations, highlighting the importance of habitat quality and law enforcement. These shrublands, largely confined to central and eastern regions of the park and isolated by unsuitable vegetation and salt plains, appear to constrain broader range occupancy. Demographic analyses revealed high initial mortality linked to translocation stress and social aggression within the acclimatisation site, and none of the wild-born individuals were likely to have survived. Cumulative survival declined over time, suggesting that repeated mortality events may threaten long-term population viability.
4. Practical implications: These findings highlight the need for adaptive reintroduction strategies, including optimising group composition, reducing translocation-related stress and social aggression, and adaptive post-release monitoring to improve survival and long-term population persistence.

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KEYWORDS

Asiatic wild ass, conservation management, demographic processes, spatial ecology, species occupancy

1 | INTRODUCTION

Megafauna have been lost in many parts of the world, but recent conservation and reintroduction commitments provide hope that these species can return to contemporary landscapes (Davoli et al., 2024). Among megafauna, large herbivores, often regarded as ecosystem engineers, play a vital role in maintaining ecosystem functioning (Jones et al., 1994). However, their populations have declined substantially in both numbers and range, primarily owing to overexploitation and habitat loss (Ripple et al., 2015). Reintroducing animals has therefore become an important conservation tool to counter these declines (IUCN/SSC Re-introduction Specialist Group, 2013). One challenge in reintroduction efforts is that the survival of the reintroduced animals in the wild is generally low (Shepherdson, 1994). As a result, it reduces the success rate of reintroduction efforts. However, survival probability can be higher if released animals are wild-born or have undergone extended acclimatisation periods within the release site (Thomas et al., 2023). Individuals selected for release under such conditions are likely to possess essential survival skills, such as heightened anti-predator behaviour or increased vigilance, which are critical after release (Thomas et al., 2023). In addition to individual traits, the location of the release site and its proximity to key landscape features can play an important role in shaping animal space use and, ultimately, population persistence. Mammalian herbivores often make trade-offs between resource acquisition and risk avoidance, leading to contrasting habitat use patterns (Bonnot et al., 2013). For example, Verzuh et al. (2024) found that helicopter hazing triggered strong and lasting avoidance behaviour in reintroduced American bison (*Bison bison*, Linnaeus 1958) in Canada, whereas encounters with humans on foot or horseback resulted in weaker responses and a greater likelihood of site occupancy. Similarly, Ghoddousi et al. (2016) showed that the spatial distribution and abundance of urials in Golestan National Park were substantially associated with proximity to ranger stations, which was used as a proxy for law enforcement intensity. Ranger stations are operational structures within protected areas that serve as bases where rangers live and work to conduct patrols, monitor wildlife, enforce regulations and respond to management and emergency needs.

In the context of reintroduction success, Sarrazin (2007a) described three key phases: establishment, growth and regulation. The establishment phase encompasses the period during which released individuals must overcome high mortality risks associated with translocation, stress and unfamiliar environments. The growth phase begins once birth rates exceed death rates and evidence of wild breeding emerges, although management interventions such as restocking may still be necessary during this phase. The regulation phase is critical for long-term persistence, reflecting a population's

capacity to sustain itself without continued human support, through interactions with the habitat and other species (Robert et al., 2015). While habitat conditions are generally expected to be the primary drivers of population growth, management actions such as the periodic translocation of individuals into reintroduced populations can also influence introduction outcomes. Despite this, limited information exists on how released animals respond to habitat features, such as vegetation communities and water availability, or how management structures like ranger stations shape occupancy patterns and behaviour (Shier, 2015). Understanding this response is particularly important for small release groups within acclimatisation centres, which may be vulnerable to demographic stochasticity, including reduced reproduction or elevated mortality, such as offspring loss caused by social aggression from dominant males (Kaczensky et al., 2021).

Long-distance dispersal into unfamiliar environments can further constrain population establishment (Armstrong & Seddon, 2008; Kaczensky et al., 2021). Management interventions such as restocking can partially offset these effects by increasing the effective initial population size. The success of such interventions depends not only on whether individuals are captive-bred or wild, but also on the number of individuals introduced (Armstrong & Seddon, 2008). Consequently, the extent to which these management practices influence survival and population growth remains an important, yet insufficiently understood, question in reintroduction biology (Robert et al., 2015).

The Persian onager (*Equus hemionus onager*, Pallas 1775) is one of five recognised subspecies of Asiatic wild ass and is currently listed as Critically Endangered (A3bcd) on the IUCN Red List, due to ongoing population declines driven by habitat loss, illegal hunting and competition with livestock (Hemami & Momeni, 2013; Kaczensky et al., 2025). Once widespread across Iran's arid and semi-arid regions, the subspecies became largely restricted by the late 20th century to a few protected areas, notably the Touran Biosphere Reserve (BR) and Bahram-e-Goor Protected Area (Hemami & Momeni, 2013; Nezami et al., 2021; Tatin et al., 2003). Long-term monitoring reveals contrasting population trajectories within these refugia. In Bahram-e-Goor, abundance increased from 84 individuals in 1975 to over 1061 by 2021, largely owing to improved protection, supplementary feeding and water provisioning (Nezami et al., 2021; Tatin et al., 2003). In contrast, the Touran population declined from 471 in 2000 (Tatin et al., 2003) to around 260 by 2025 (DoE, 2022), highlighting persistent challenges to population growth. Comparable patterns occur across Central Asia, where wild ass populations are fragmented and subject to demographic bottlenecks (Kaczensky et al., 2018). Targeted conservation interventions have stabilised some populations, demonstrating the potential for active management to reverse declines in harsh desert environments (Nezami

et al., 2021). Despite these efforts, knowledge remains limited regarding how reintroduced onagers respond to habitat features and management interventions, such as vegetation communities, water sources or ranger stations, and how these factors influence survival, occupancy and population growth. In this study, we evaluate the demographic dynamics and occupancy patterns of the reintroduced Persian onager in Kavir National Park, providing insights into how management interacts to shape establishment in fragmented desert landscapes.

In this study, we addressed two main research questions: (i) How are the occupancy patterns of reintroduced Persian onagers shaped by trade-offs between key habitat characteristics (e.g. vegetation community, water troughs) and the spatial distribution of ranger stations? and (ii) To what extent do management interventions, including periodic restocking and group composition, influence survival and population growth both within the acclimatisation centre and after release into the wild in Kavir National Park?

2 | MATERIALS AND METHODS

2.1 | Study area

In Iran, onagers now persist in two indigenous populations. The southern population is primarily confined to Qatrouiyeh National Park, which lies within the Bahram-e-Goor Protected Area in south-central Iran (Kaczensky et al., 2025). The central-northern population occurs as a separate group in the Touran Biosphere Reserve.

In addition to these indigenous populations, reintroduced groups are also present in Kalmand Protected Area and Siah-Kooh National Park (Kaczensky et al., 2018).

Our study was conducted in the Kavir National Park, which, together with Kavir Protected Area, forms Kavir Biosphere Reserve covering 6810.68 km². Of this, 2453.04 km² was designated as the Kavir Protected Area in 1964, and a further 4357.64 km² was declared Kavir National Park in 1976. This reserve is located on the north-western edge of the Dasht-e Kavir desert, a vast basin within Iran's central plateau (Rechinger & Wendelbo, 1976; Figure 1). Several mountain ranges occur within the region, including Siah Kouh, Kouh-e Siah and Kouh-e Sefidab, with elevations ranging from 740 to 1865 m. Seasonal rivers, such as Shekar-Ab, Jarjaro river and Kolo rivers, originate in these mountains and extend into extensive floodplains. Geologically, the region represents a depression of Iran's central plateau, with extrusive igneous rocks dominating the higher elevations. A large salt lake (Daryach-e Namak ~2000 km²) lies to the west of the park, outside its boundaries. Within the park, several freshwater and brackish springs emerge at the foothills of the Siah-Kuh Mountains. Annual precipitation ranges from 50 to 300 mm, while temperatures reach 40–50°C during the hot months of June, July and August, and may drop to as low as –15°C in winter (Rechinger & Wendelbo, 1976; Figure 1). The park is devoid of permanent human settlements and remains an important stronghold for native wild mammalian fauna. Historically, the Asiatic wild ass (onager, *Equus hemionus*) persisted in the region but went extinct in the wild within this area in 1983. Other species present include Jebeer gazelle (*Gazella bennettii* Sykes, 1831), wild sheep (*Ovis vignei*

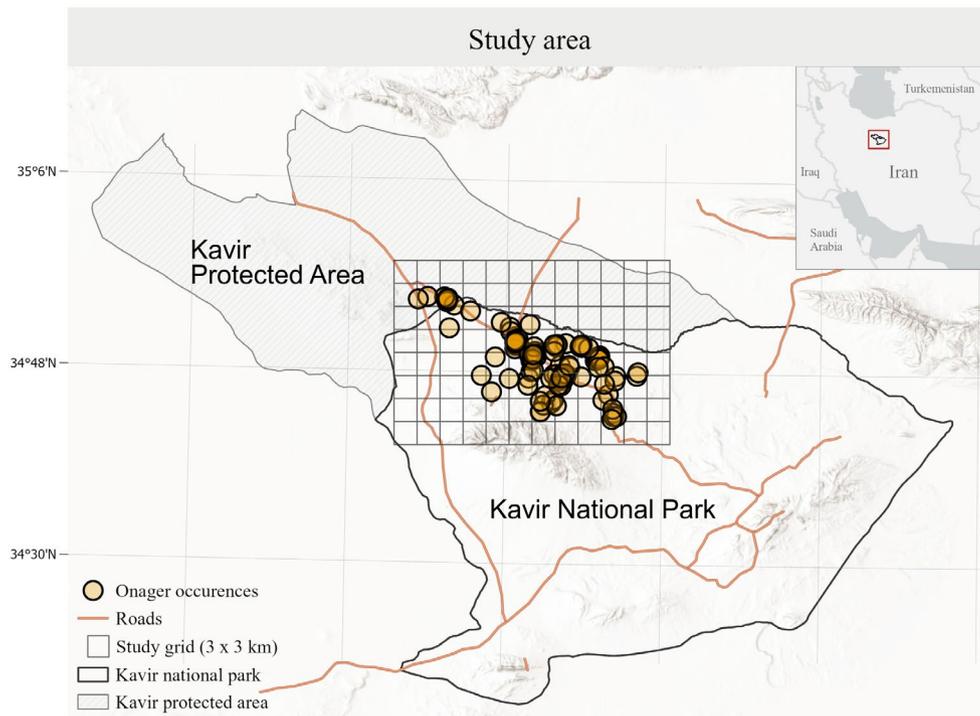


FIGURE 1 Map of the study area covering parts of Kavir National Park and Kavir Protected Area, Iran, showing the 4×4 km grid cells used for surveys and occurrences of the reintroduced Persian onager.

Blyth, 1841), bezoar goat (*Capra aegagrus* Erxleben, 1777), Persian leopard (*Panthera pardus tulliana*, Valenciennes, 1856), grey wolf (*Canis lupus*, Linnaeus, 1758), Blandford's fox (*Vulpes cana*, Blanford, 1877), sand cat (*Felis margarita*), striped hyena (*Hyaena hyaena*, Linnaeus, 1758) and Rüppell's fox (*Vulpes rueppellii*, Schinz, 1825) (O'Regan, 1980; Yusefi et al., 2019).

2.2 | Study design

We restricted our study area to the north-western portion of Kavir National Park (Category II IUCN), as onagers are currently confined to this part of the park and to the south-eastern section of the Kavir Protected Area (Category V IUCN; Figure 1). Consequently, the southern and eastern sections of the park, where onagers are absent, were excluded from the analysis. We overlaid $4 \times 4 \text{ km}^2$ cells ($n=96$, sampling units) covering a total area of 153,600 ha and encompassing the entire known range of the reintroduced onager population. The selected grid resolution represented a compromise between survey effort (ranger patrol coverage), detection probability and the daily movement patterns of the species (Soofi et al., 2022). More than two-thirds of the study area lies within Kavir National Park, and the north-western extent of the surveyed onager range overlaps with the Kavir Protected Area (Figures 1 and 2).

2.3 | Data collection

The daily surveys were conducted from December 2022 to August 2023, commencing between 5:00 and 6:00 and ending at 19:00 and

20:00 (Soofi et al., 2026). Surveys consisted of a combination of on-foot, motorbike and vehicle patrols within grid cells. Direct sightings of onagers were recorded using binoculars and an offline GPS mobile application. Data collection was conducted as part of the second author's master's thesis under research permit No. 2025/95 issued by the Iranian Department of Environment.

2.4 | Modelling approach

We analysed onager's detection and non-detection data using a single-season occupancy model (MacKenzie et al., 2002) implemented within a Bayesian framework. A typical survey protocol for occupancy models involves visiting sampling sites and spending time (i.e. survey effort) at each site to search for individuals of the target species or evidence of their presence (e.g. sightings or signs). Each site must be surveyed more than twice to allow for the estimation of the detection probability parameter (p) (MacKenzie et al., 2002). We modelled probability of true occurrence Z_i (an unobserved latent variable) of onagers in cell i as a Bernoulli random variable with logit link function (MacKenzie et al., 2002):

$$Z_i \sim \text{Bernoulli}(\psi_i)$$

True occupancy state Z has two possible values: occupied ($Z=1$) and unoccupied ($Z=0$) (Royle & Kéry, 2007).

The observed detections (sightings) of Persian onagers y_{ij} at survey j (each month was defined as an occasion) are also an outcome of a Bernoulli random variable for defined conditional on Z_i :

$$y_{ij} | Z_i \sim \text{Bernoulli}(Z_i p_{ij})$$

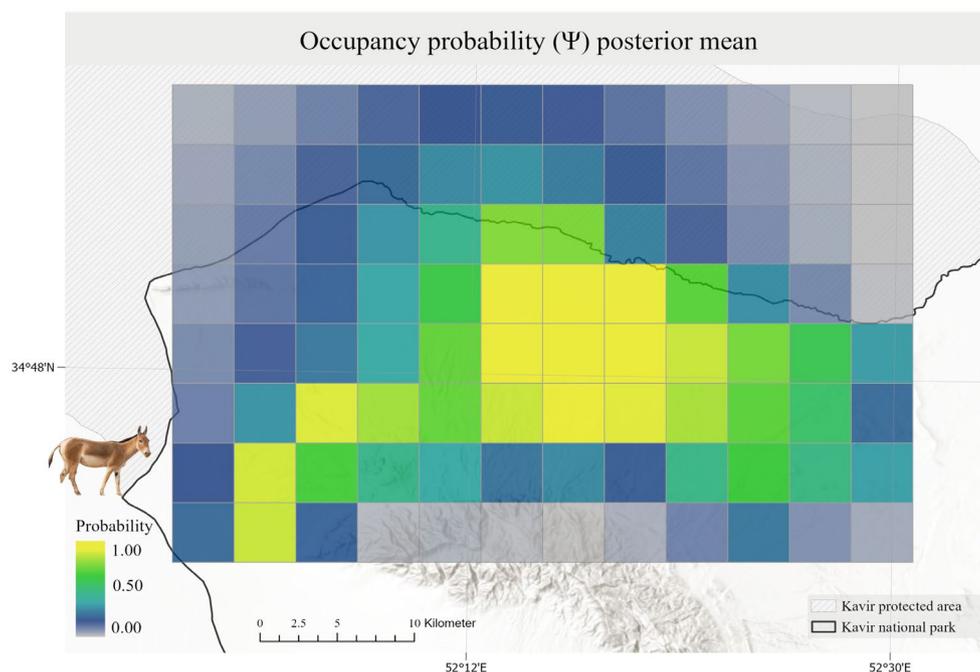


FIGURE 2 Predicted posterior mean occupancy probability of the reintroduced Persian onager across the study area, derived from the best-fitting Bayesian occupancy model.

Thus, if a cell is occupied ($Z=1$), we detect onagers with probability p_{ij} whereas, if the cell is not occupied ($Z=0$), then $y=0$ with probability 1.

In the detection probability (p) model, we included covariates (Table 1) that were thought to influence detections using a logit-linear model:

$$\text{logit}(p_{ij}) = \alpha_0 + \alpha_1 \cdot X_{1,ij} + \alpha_2 \cdot X_{2,ij}^2 + \dots + \alpha_q \cdot X_{q,ij}$$

where p_{ij} is the probability of detecting onager at site i during survey j , α_0 denotes intercept, and $\alpha_1, \dots, \alpha_q$ are the regression coefficients of the detection parameter to be estimated. $X_{1,ij}, \dots, X_{q,ij}$ are site-level covariates that are assumed to influence onager detection probability.

To assess whether and how the occupancy (ψ) of onagers is influenced by habitat characteristics (e.g. vegetation types) and management relevant variables (e.g. ranger stations) we considered a set of hypotheses (Table 1) and our best-fitting model can be described as:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 \cdot X_{1,i} + \dots + \beta_2 \cdot X_{2,i} + \beta_p \cdot X_{p,i}$$

where ψ_i is the probability that site i is occupied, β_0 represents the intercept and β_1, \dots, β_p are the regression coefficients of occupancy to

be estimated, and $X_{1,i}, \dots, X_{p,i}$ are covariates describing variation in occupancy across sites.

2.5 | Detection covariates

For detection probability, we included the linear effect of Julian day to represent temporal variation across survey period (December 2022–August 2023). To allow for non-linear seasonal patterns in detectability, we also incorporated a quadratic term for Julian day. Survey effort, measured as distance travelled (km), was included to account for variation in detection arising from unequal survey effort. Effort was standardised by dividing the total distance travelled by the number of grid cells surveyed during each sampling occasion (Table 1).

2.6 | Occupancy covariates

Here we modelled the logit transformed occupancy as a linear function of hypothesised environmental and management covariates (Table 1). Mean elevation (m) was calculated for each grid cell using a digital elevation model of the study area and the Zonal Statistics as

TABLE 1 Predictor variables, their descriptions, units and associated hypotheses used to model occupancy of reintroduced Persian onagers in Kavir National Park and the Kavir protected area in Iran.

Predictor variables	Description and unit	Expected effect
Julian day	Day of year (1–365), December 2022 to August 2023	Onager occurrence is expected to vary across survey period
Julian day ²	Quadratic effect of Julian day	Onager observations follow a non-linear seasonal pattern, with peaks during periods of breeding and movement
Survey effort	Total distance surveyed (km) per sampling unit	Detection probability of onagers increases when survey effort increases
Distance to water trough	Distance (m) from each onager occurrence location to the nearest water trough	Onagers are more likely to be observed near water sources, particularly during the drier season
Distance to ranger station	Distance (m) from each onager's occurrence points to the nearest ranger station	Onager occupancy is higher near ranger stations, likely due to habituation to regular patrolling or attraction to resources, as individuals were previously held in a captive site near these ranger stations before release
<i>Artemisia-Zygophyllum</i>	Percentage (%) of each grid cell covered by <i>Artemisia-Zygophyllum</i> vegetation	Onagers preferentially occupy areas dominated by the <i>Artemisia-Zygophyllum</i> plant community, which provides favourable foraging conditions
<i>Artemisia-Stipa</i>	Percentage (%) of each grid cell covered by <i>Artemisia-Stipa</i> vegetation	Onagers show higher occupancy in areas dominated by the <i>Artemisia-Stipa</i> plant community, indicating a preference for this vegetation type
Salt-land	Total salt-land area (km ²) within each grid cell	Occupancy is lower in saline areas, due to limited forage availability

Table tool in Arc GIS Pro. Distances to the nearest water troughs and ranger stations were quantified as the mean Euclidean distance from each grid cell to these features. Land cover was characterised using the vegetation classification provided by the Kavir National Park. Salt lands (temporarily dry areas with underlying moisture) were included as distinct land cover class, and their proportional coverage per grid cell was calculated using the Zonal Statistic as Table tool.

For all vegetation classes, coverage was calculated as the percentage of each grid cell and normalised by grid cell area (Table 1). Four dominant vegetation types were identified: *Artemisia sieberi*–*Zygophyllum*, *Artemisia*–*Seidlitzia*, *Artemisia*–*Zygophyllum*–*Seidlitzia* and *Artemisia*–*Dendrostellera* (Supporting Information). In addition, Euclidean distances from onager occurrence locations to the nearest ranger stations and water troughs were calculated using ArcGIS Pro (ESRI, 2024).

2.7 | Statistical analyses

We fitted our models using the 'ubms' R package (Kellner et al., 2022) via Stan (Stan Development Team, 2024) in R v. 4.4.1 (R Core Team, 2024). We specified normal priors (mean $\mu = 0$, scale $\sigma^2 = 1$) for the regression coefficients and intercepts in both the detection and occupancy sub-models (Kellner et al., 2022; Royle & Dorazio, 2008). Posterior distributions were estimated using Markov chain Monte Carlo (MCMC) with four parallel chains of 5000 iterations each, producing a total of 20,000 posterior samples (Kellner et al., 2022). Lastly, we checked our model fit, by plotting the residuals against the fitted values using `plot_residual` function and posterior predictive checks (Kellner et al., 2022; Figures S1 and S2).

2.8 | Modelling

We first fitted a null model, then sequentially added one covariate to the detection sub-model, while keeping the occupancy sub-model constant (Kéry & Royle, 2016). Subsequently, we expanded both sub-models concurrently by adding covariates in the detection 'p' parameter (i.e. Julian day, quadratic term of Julian day, survey effort, distance to ranger stations, from December 2022 to August 2023). Similarly, in the occupancy sub-model we fitted a linear effect of vegetation type, distance from onager occurrence points to ranger stations, distance to water troughs, elevation and area size of salt marshes (Table 1). We ranked our models using the leave-one-out (LOO-CV) cross-validation method (Vehtari et al., 2017; Table S1), which evaluates out-of-sample predictive accuracy from within-sample fits (Vehtari et al., 2017). We interpreted coefficients as substantial when their Bayesian credible interval (BCI) did not include zero, less substantial if the coefficients interval marginally included zero, and non-substantial otherwise (Benjamin et al., 2018). We assessed goodness-of-fit using two approaches (Kellner et al., 2022): posterior predictive checks, drawing 5000 posterior samples and computing MacKenzie and Bailey (2004) statistic for observed and simulated datasets (Kellner et al., 2022) and residual-based methods

(Wright et al., 2019), which calculates residuals separately for the occupancy and detection sub-models (Gelman & Hill, 2007).

2.9 | Population demographic analysis

We estimated the annualised finite rate of increase (λ) of onagers between two monitoring years using the logarithmic average of proportional change in abundance. Specifically, for a population with size N counted at two time points t_1 and t_2 the rate over the interval.

$\Delta T = t_2 - t_1$ was calculated as:

$$\lambda t = \left(\frac{N_{t_2}}{N_{t_1}} \right)^{1/t_2 - t_1},$$

where a λ value greater than 1 indicates an increasing trend, a value less than 1 indicates a declining trend, and a value equal to 1 indicates a stable population (Smith, 2015).

We applied the Kaplan–Meier (KM) survival probability method to estimate annual survival rates. This approach was appropriate because all deaths were known (Smith, 2015). Monitoring of onagers in Kavir National Park relied on daily ranger patrol records, which included behavioural observations, births, juvenile and adult deaths, numbers of restocked individuals and their origins (i.e. wild-born or captive-bred). Data were consistently compiled across multiples stages, including capture, translocation, acclimatisation and release into the wild.

The KM approach accommodates multiple intervals of sampling and staggered entry, allowing animals gradually released over time to contribute to estimates of annual survival probability (S_t). Survival probability (Smith, 2015) can be expressed as:

$$S(t) = \prod_{i=1}^t \left[1 - \left(\frac{i - d_i}{i - n_i} \right) \right],$$

where d_i is the number of deaths and n_i is the number of onagers at risk in year i , S_t is the survival probability at year t , and Π is the multiplication operator (Smith, 2015). The product of these annual survival probabilities gives the cumulative survival probability (S_{cum}), that is, the probability that an individual survives from the start of the study up to year t . Because this multiplies numbers less than 1, cumulative survival declines over time even if annual survival S_t is high (Smith, 2015). In contrast, the population growth rate (λ) reflects the net change in population abundance, including births and restocking, and can increase even when some individuals die (Smith, 2015).

3 | RESULTS

3.1 | Detection

Our detection sub-model for the best-fitting model indicated a concave response ($\beta_{\text{Julian day}^2} = -0.74$, 95% BCI = -1.17 to -0.36 and $\beta_{\text{Julian day}} = 0.15$, BCI = -0.21 to 0.51) (Figures 3a and 4a). Thus, detection probability peaked in June–July and then sharply declined afterward (Table 2, Figure 3a). The survey effort had a substantial and positive

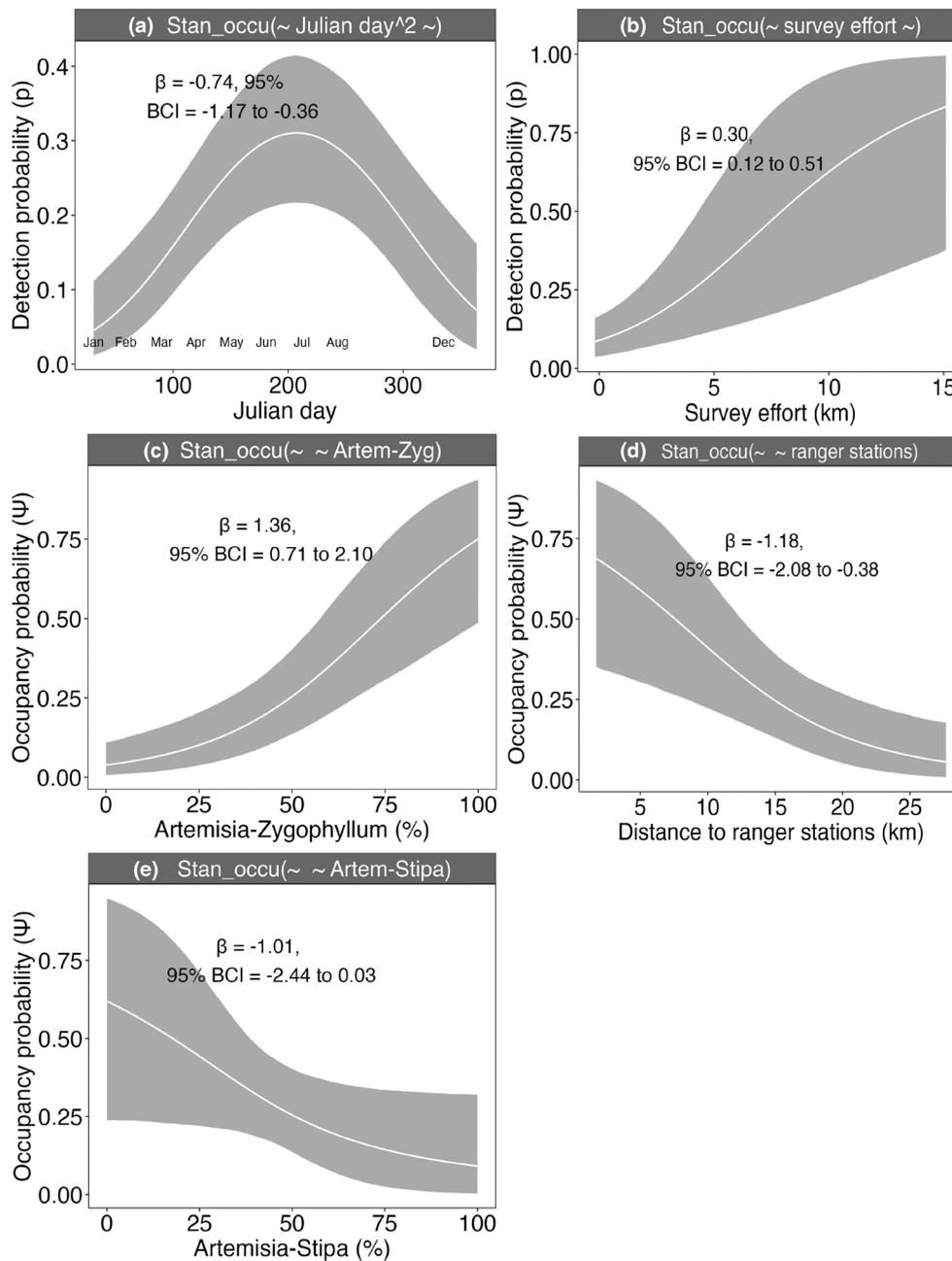


FIGURE 3 Response curves estimated from the best-fitting model of expected detection of introduced (in 2018) Persian onager in relationship with (a) Julian day (December 2022–2023), (b) survey effort, (c) expected occupancy probability with vegetation type (*Artemisia-Zygophyllum*) (%), (d) ranger stations (km) and (e) *Artemisia-Stipa* (%) vegetation type. The olive-green shaded colour illustrates the Bayesian credible interval (BCI), and the white solid lines colour show the posterior mean estimate.

effect ($\beta_{\text{survey effort}} = 0.30$, 95% BCR = 0.12 to 0.51) (Table 2; Figures 3b and 4a). Detection is likely to reach 100% at a survey effort of approximately 15 km (Figures 3b and 4a). This implies that the longer the survey effort (up to 15 km), the more likely it is to detect an onager.

3.2 | Occupancy

The predicted posterior mean occupancy of Persian onagers varied across the studied area (Figure 2), with higher probabilities in

the north-western portions of the park and areas near *Artemisia-Zygophyllum* vegetation patches. Water troughs did not affect onager occupancy ($\beta_{\text{distance to water troughs}} = 0.02$, 95% BCR = -0.92 to 0.94; Figure 4b). In contrast, *Artemisia-Zygophyllum* vegetation had a strong positive effect on occupancy ($\beta_{\text{Artemisia-Zygophyllum}} = 1.36$, 95% BCI = 0.71, 2.10; Table 2; Figure 3c). Ranger stations had a notable negative effect ($\beta_{\text{distance to ranger station}} = -1.18$, 95% BCR = -2.08 to -0.38; Figure 3d), indicating that occupancy is relatively high near ranger stations but declines sharply to near zero at distances of around 25 km (Figure 3d). Finally, *Artemisia-Stipa* vegetation tended to

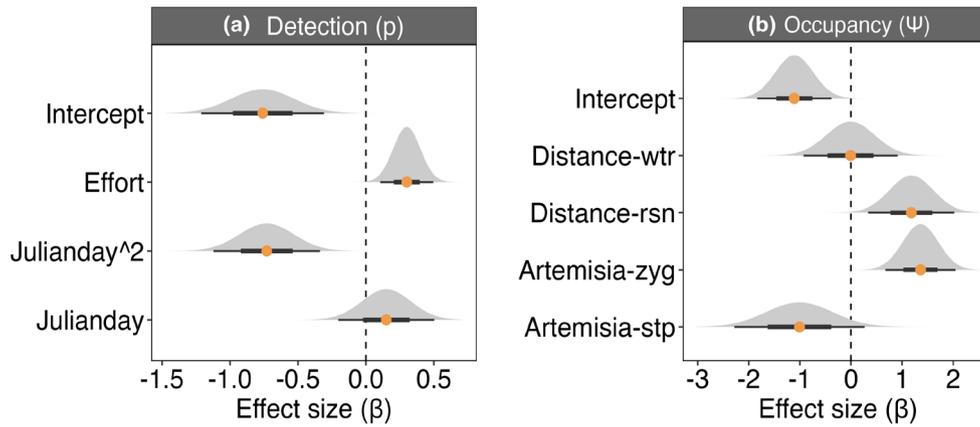


FIGURE 4 Effect sizes of detection (a) and occupancy (b) covariates for reintroduced Persian onagers in Kavir National Park. In the detection panel Julianday represents the survey period from December 2022 to August 2023. Julianday² indicates the quadratic term. In the occupancy panel, *Distance-wtr* is the distance to water troughs, *distance-stn* indicates the distance to ranger stations, *Artemisia-zyg* denotes *Artemisia-Zygophyllum* and *Artemisia-stp* refers to *Artemisia-Stipa* vegetation types.

Model parameters	Estimates (β)	SD	2.5%	97.5%	n_eff	Rhat
Detection probability (p)						
$\alpha_{\text{intercept}}$	-1.11	0.23	-1.22	-0.31	7414	1.00
$\alpha_{\text{julianday}}$	0.15	0.18	-0.21	0.51	12,055	1.00
$\alpha_{\text{julianday}}^2$	-0.74	0.20	-1.17	-0.36	8968	1.00
$\alpha_{\text{survey effort (km)}}$	0.30	0.10	0.12	0.51	10,047	1.00
Occupancy probability (ψ)						
$\beta_{\text{intercept}}$	-1.11	0.37	-1.84	-0.40	9952	1.00
$\beta_{\text{distance to water troughs}}$	0.02	0.47	-0.94	0.92	7730	1.00
$\beta_{\text{Artemisia-Zygophyllum}}$	1.36	0.35	0.71	2.10	8638	1.00
$\beta_{\text{distance to ranger stations}}$	-1.18	0.43	-2.08	-0.38	7061	1.00
$\beta_{\text{Artemisia-Stipa}}$	-1.01	0.65	-2.44	0.03	8741	1.00

TABLE 2 Summary of the best-fitting single-season occupancy model implemented for introduced Persian onagers in Kavir National Park, Iran.

Note: Parameter estimates are reported as Bayesian posterior means (slope β , α), standard deviations (SD) and 95% credible intervals (BCI). Rhat represents the Gelman–Rubin convergence diagnostic value, while n_eff denotes the effective sample size. Parameters with BCIs that do not overlap 0 are considered to have a substantial effect.

reduce occupancy ($\beta_{\text{Artemisia-Stipa}} = -1.01$, 95% BCI = -2.44 to 0.03; Table 2; Figures 3e and 4b), although the effect was less substantial, as the credible interval slightly overlapped zero.

3.3 | Population demographic and translocations

Of the 10 onagers translocated in 2018 from Touran National Park to an acclimatisation site in Kavir National Park, five died during the capture and translocation process (Table 3). To compensate for these losses, four additional individuals (three females and one male), also originating from Touran but held at the Gourab captive breeding facility in Yazd Province, were introduced (Table 3). This brought the initial reintroduction group to seven females and two males. Survival probability during the translocation phase was significantly reduced ($S_t = 0.50$; Table 3; Figure 5). After the

release into the wild in November 2020, offspring survival improved to 0.94 in 2021. Notably, the dominant male retained during the acclimatisation phase was responsible for the deaths of three foals and one adult male, and one additional foal was killed by a female, likely due to intraspecific aggression. Following release, only one foal was killed by wolves near a spring, and three others died during or shortly after birth, likely due to underlying genetic issues. Survival probability during the translocation phase was notably reduced ($S_t = 0.50$; Table 3; Figure 5), resulting in a decline in cumulative survival (S_{cum}) during the early years of the reintroduction program, even though annual survival improved in subsequent years.

Between 2019 and 2024, the reintroduced onager population showed a steady increase, with annual population growth rates (λ_t) ranging from 1.10 to 1.93. The highest growth rate was recorded in 2022, coinciding with the restocking of 12 captive-born individuals

TABLE 3 Summary of population dynamics of reintroduced Persian onagers in Kavir National Park, Iran.

Year	N_t	Birth	Juvenile death	Restocking	Death	Origin	λ_t	S_t	S_{cum}
2018	10				5	Captive-bred Touran NP			
2018	9	0	0	4		Captive-bred Gourab & Touran BR		0.50	
2019	10	4	3				1.11	0.77	0.77
2020	11	4	3				1.10	0.79	0.61
2021	15	5	1				1.36	0.94	0.57
2022	29	4	1	12	1	Captive-bred Khabr NP	1.93	0.94	0.53
2023	35	6	1	3	2	Wild-born Touran BR	1.21	0.92	0.49
2024	42	9	1				1.20	0.98	0.48

Note: N_t denotes annual population size. λ_t the annual population growth rate (i.e. rate of change), S_t the annual survival probability and S_{cum} the cumulative survival probability. Data include numbers of births, juvenile and adult deaths, individuals added through restocking and mortality among restocked individuals. In 2018, ten onagers were translocated from Touran Biosphere Reserve (BR) to the acclimatisation site in Kavir National Park (NP). Following the death of five individuals during this process, four individuals were restocked later that year from the Gourab captive breeding centre.

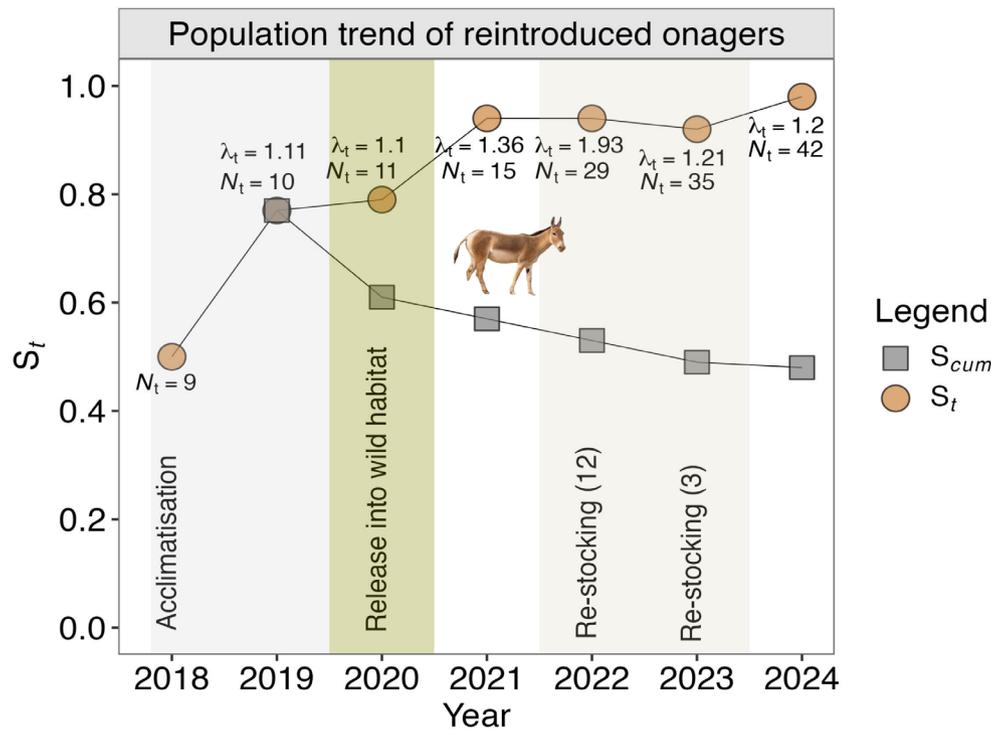


FIGURE 5 Annual survival probability (S_t , orange solid circle) of reintroduced Persian onagers in Kavir National Park, Iran. N_t indicates the population size in each year, S_{cum} indicates the cumulative survival probability, and lambda λ_t denotes the annual population growth rate.

(six female, three males, three immatures with undefined sex), one of which died due to aggression from the dominant male. These individuals originated from Khabr National Park, in Kerman province. Annual survival probability (S_t) varied across years, from a low of 0.50 in 2019 to a high of 0.98 in 2024 (Table 3, Figure 5). Higher survival rates generally corresponded with reduced adult mortality and consistent recruitment through both births and translocations. In contrast, the 2023 translocation of three wild-born onagers was

unsuccessful. Following their dispersal from the acclimatisation site, one female was found dead under unknown circumstances, while another individual could not be located. The remaining male dispersed 70–80km beyond the park boundary, became trapped in a salt lake, and was later recaptured and returned to the acclimatisation site. Additionally, one male born in Kavir National Park was translocated to a captive breeding facility in Yazd Province to support genetic exchange.

4 | DISCUSSION

Reintroduction is a key conservation priority aimed at restoring viable populations of native species within their historical ranges through the release of wild or captive-bred individuals (IUCN/SSC Re-introduction Specialist Group, 2013; Seddon et al., 2007). Yet, knowledge remains limited regarding how released groups respond to habitat characteristics and management actions, and how population persistence is shaped by interventions such as manipulation of group composition or repeated restocking during establishment and growth phases (Armstrong & Seddon, 2008; Robert et al., 2015). Here we focused on a unique and large desert landscape in central-north Iran that is largely devoid of human pressure. In the detection sub-model, we found a substantial seasonal pattern, with onager detection probability peaking in early summer (June–July) and declining sharply from August onwards. The quadratic effect of Julian day indicates a non-linear detectability pattern, likely driven by interacting behavioural and environmental factors. One possible explanation relates to reproductive timing, as Persian onagers predominantly give birth in June and July. During this period, females may increase activity levels or utilise more open habitats, potentially to access high-quality forage required for lactation, thereby increasing their visibility during foot-based surveys. In contrast to sympatric ungulates such as jebeer gazelles, which seek shade in vegetation such as *Haloxylon* spp.; a behaviour documented in the park by O'Regan (1980), onagers do not appear to exhibit similar shading behaviour. Finally, detection probability increased with survey distance, suggesting the importance of effort-standardised monitoring protocols.

Contrary to our expectations, we found no substantial effect of proximity to water troughs on occupancy of onagers, despite the arid environment in Kavir National Park. This may be explained by the onagers' physiological adaptation to dry environments or the availability of alternative water sources such as ephemeral pools or moisture-rich plants (Boyd & King, 2019). In contrast, onagers' occupancy was strongly associated with the *Artemisia-Zygophyllum* plant community, which likely offers both foraging opportunities and protection from predators (O'Regan, 1980). Our results corroborate O'Regan's findings from 1974 to 1977, who conducted repeated population estimations and habitat preference analyses of onagers using aerial and road transects. He concluded that onagers in the park significantly occupy *Artemisia-Zygophyllum*-only habitats but avoid calcareous lithosols (soil type) and *Seidlitzia* and *Haloxylon* vegetation types, and that they do not use these plants for shade even during the hottest days of summer. The *Artemisia* community largely covers the alluvial plains, whereas the *Zygophyllum* community occurs on drier soils. These vegetation communities are restricted to small patches in the central and eastern parts of the park and are isolated by less suitable vegetation and salt plains in the northern areas (O'Regan, 1980). It is likely that such limitations in their preferred vegetation communities have reduced their recolonisation (occupancy) of broader areas within the park. Our findings further showed that onagers tended to occur closer to ranger stations.

Specifically, onager occupancy increased by over 50% within a 5 km distance of ranger stations, with occupancy probability declining markedly beyond 25 km. This finding is in line with an earlier study by Ghoddousi et al. (2016), which found that ungulates in Golestan National Park tended to occur at higher abundances closer to ranger stations, presumably due to the perceived safety from illegal hunting activities in the mountainous steppes. This pattern may reflect variation in law enforcement intensity, as areas closer to ranger stations likely receive more frequent patrols, which may both reduce illegal hunting and increase onager detection. However, because the onagers were captive-born, their prior exposure to rangers around the acclimatisation centre may also have shaped their behavioural responses. Familiarity with ranger presence could promote tolerance of human activity and encourage individuals to remain closer to ranger stations (Berger-Tal & Saltz, 2014). One potential consequence of such spatial association is reduced dispersal, which may limit the exploration and colonisation of other suitable habitats, and lead to locally concentrated grazing pressure (Berger-Tal & Saltz, 2014). Similarly, Jachmann (2008) showed that areas surrounding ranger stations can function as refugia for large mammals, such as elephants, by lowering predation risk. We therefore surmise that onagers may associate ranger-patrolled areas with indirect protection or with supplementary resources near the acclimatisation site (Stien et al., 2013). Nevertheless, our models did not explicitly account for these mechanisms, and this interpretation should be treated with caution. Finally, the negative, though less substantial, effect of *Artemisia-Stipa* vegetation on onagers' occupancy may indicate differences in forage quality or vegetation structure, highlighting the need for finer-scale studies on forage selection and dietary ecology in this landscape.

Our demographic analysis provides important insights into the population development of Persian onagers. The translocation process posed substantial challenges during the acclimatisation phase, with 50% adult mortality attributable to the stressful conditions associated with capture and translocation (Armstrong & Seddon, 2008; Berger-Tal et al., 2020). In addition, intraspecific aggression by a dominant male contributed to 13% of offspring mortality during acclimatisation, highlighting the importance of managing social structures during this critical period (Moseby et al., 2014). One foal was also killed by a female, possibly due to resource limitation in captivity. Following release into the wild, juvenile survival probability increased markedly and coincided with a notable rise in population growth rate (λ), particularly after the restocking of captive-born individuals in 2022. Consequently, population growth became consistently positive, with a peak observed in 2022, driven by both reduced juvenile mortality and higher adult survival. Overall, these results indicate that reintroduced onagers are successfully reproducing in the wild and progressively adapting to their new environment. The high foal mortality observed during the acclimatisation further highlights the critical role of managing social dynamics and animal behaviour in the early stages of reintroduction (Linklater et al., 2010).

Our results show that the 2023 translocation of three wild-born onagers was unsuccessful, with one female found dead, one

individual missing and a male dispersed far beyond the park boundary before being recaptured. This highlights the challenges of reintroducing free-ranging animals that may be less adapted to captivity and management environments. A similar pattern was reported by Kaczensky et al. (2021) in Kazakhstan, where reintroduced kulan showed low social cohesion after release. Despite initially forming cohesive groups in pre-release enclosures, the animals dispersed across the vast steppe, with no successful reproduction recorded and some individuals being shot illegally or dying naturally. Kaczensky et al. (2021) further noted that the absence of conspecifics, the large reintroduction ranges, and a lack of movement-constraining factors contributed to fission–fusion dynamics, preventing the formation of stable social groups in the wild.

In contrast to free-ranging onagers, captive-born individuals showed a relatively higher survival probability. This apparent advantage may reflect their larger group size, which helped maintain social cohesion, as well as their captive-born origin, which may have increased their tolerance of management interventions and facilitated adaptation to the release environment (Berger-Tal et al., 2020; Moseby et al., 2014). In contrast, wild-born onagers experienced greater challenges following release in 2023, including dispersal and elevated mortality, highlighting the difficulties associated with reintroducing individuals that have not been acclimatised to captive or semi-captive conditions. Overall, our findings emphasise the importance of social structure, habitat conditions and management strategies (Armstrong & Seddon, 2008) in shaping the success of Persian onager reintroduction efforts.

5 | CONCLUSIONS

Our findings provide valuable insights for the conservation management of reintroduced Asiatic wild ass in arid desert ecosystems. The results highlight the importance of optimising monitoring strategies by aligning survey efforts with seasonal variation in detectability. Onagers occurred predominantly in *Artemisia-Zygophyllum* shrublands, which are limited to small, spatially isolated patches separated by unsuitable vegetation and extensive salt plains. Such habitat fragmentation likely constrains their ability to recolonise larger areas of the park, emphasising the need importance to conserve these plant communities to support long-term population persistence. Occupancy was also higher near ranger stations, suggest they benefit from law enforcement activities or habituation to the presence of rangers, potentially reducing predation risk. Demographic analyses showed that adult mortality was highest during capture and translocation, whereas foal mortality peaked during the acclimatisation phase, mainly due to social aggression from a dominant male; additionally, one foal was killed by a female, resource limitation under captive conditions. Survival rates improved substantially following release into the wild. Furthermore, captive-born individuals contributed positively to population growth, while wild-caught translocated onagers experienced higher mortality and dispersal, limiting their effectiveness in reintroduction

programmes. These findings highlight the importance of carefully structuring release groups, selecting restocking individuals based on origin (wild-born vs. captive-bred), and the value of implementing adaptive post-release monitoring. Appropriate group composition can minimise intraspecific aggression, promote social cohesion and enhance survival during critical early phases such as acclimatisation and initial release (Moseby et al., 2014). Individuals with prior exposure to captivity or structured management may be better adaptable to cope with reintroduction conditions, showing higher survival and reduced post-release dispersal compared with wild-born translocated animals (Berger-Tal et al., 2020). Comparable challenges have been documented in reintroductions of Central Asian wild asses, where weak social cohesion and extensive dispersal constrained establishment success in free-ranging kulan populations (Kaczensky et al., 2021). Collectively, these findings emphasise the importance of continuous post-release monitoring, which allows early detection of mortality, dispersal or behavioural disruptions and enables timely management interventions to support population growth and long-term persistence in fragmented desert landscapes. Although survival was initially low due to translocation-related stress, it progressively improved following release into suitable wild habitat. Finally, our findings suggest that reintroduction policies incorporate adaptive management by considering the origin of restocked individuals and ensuring appropriate group composition to enhance survival and support population growth.

AUTHOR CONTRIBUTIONS

Mahmood Soofi and Mehdi Lahordi conceived the study and designed the methodology. Fieldwork was conducted by Mehdi Lahordi, who is a ranger in Kavir National Park, together with two additional park rangers who carried out regular daily patrols. Mahmood Soofi conducted statistical analysis, and Jan Niklas-Trei prepared the spatial data. This study formed part of Mehdi Lahordi's Master's thesis. All authors contributed critically to manuscript drafts and approved the final version for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data generated through this work are archived in Figshare data repository at <https://doi.org/10.6084/m9.figshare.31423124> (Soofi et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Shows residual plots of the occupancy sub-model obtained with function plot_residual.

Figure S2. The left histogram compares the proportion of zeros in the simulated data with that in the actual dataset. The right panel shows the posterior predictive check plot, with a Bayesian p -value of 0.091, indicating good model fit.

Table S1. Model comparison (Leave-one-out cross validation technique) based on covariates influencing detection (p) and occupancy (Ψ) parameters with corresponding expected log predictive density (elpd), difference in elpd (elpd_diff), and standard error of the difference (se_diff).

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