Animal Conservation

ORIGINAL RESEARCH OPEN ACCESS

Population Viability Analysis to Inform Reintroduction Decisions for a Group-Living Primate, the Barbary Macaque

Elisa Neves[1] | Sarah Le Berre[1,2] | Sidi Imad Cherkaoui[3,4] | Jasper Iepema[3] | Zouhair Amhaouch[5] | Brahim Ismaili[6] | Latifa Sikli[5] | Nelly Ménard[1] | Pascaline Le Gouar[1]

[1]UMR 6553, ECOBIO: Ecosystems, Biodiversity, Evolution, CNRS/University of Rennes 1, Biological Station of Paimpont, Paimpont, France | [2]Chair of Silviculture, Institute of Silviculture and Forest Protection, TUD Dresden University of Technology, Tharandt, Germany | [3]AAP Morocco, Animal Advocacy and Protection, Almere, the Netherlands | [4]Département de Zoologie et Ecologie Animale, Institut Scientifique de Rabat, Mohammed V University, Rabat, Morocco | [5]Agence Nationale Des Eaux et Forêts, Rabat-Agdal, Morocco | [6]Tazekka National Park, Taza, Morocco

Correspondence: Elisa Neves (elisa.neves7@gmail.com)

Received: 15 May 2024 | **Revised:** 26 March 2025 | **Accepted:** 1 April 2025

Editor: John Ewen | **Associate Editor:** Aldina Franco

Funding: This work was supported by Animal Advocacy and Protection and Centre National de la Recherche Scientifique, IRP project DIERCOMA.

Keywords: extinction risk | *Macaca sylvanus* | population viability analysis | reintroductions | release costs | soft-release

Analyse de viabilité de population | réintroduction | coûts de réintroduction | risque d'extinction | soft-release | *Macaca sylvanus*

ABSTRACT

Demographic analyses provide valuable insights that can significantly enhance reintroduction planning and decision-making, helping to improve the likelihood of reintroduction success. We developed a model to evaluate the chances of success for a re-introduction of the endangered Barbary macaque (*Macaca sylvanus*). The model incorporates age-specific vital rates estimated from 11 years of demographic data on a wild population, reductions in survival and reproduction due to potential release costs, demographic and environmental stochasticity, reinforcement releases, and catastrophic events. Based on the available individuals considered as best candidates for reintroduction, we compared extinction risks under two release strategies. One strategy entails releasing all individuals as one large social group, while the other entails forming and releasing two smaller, separate groups. Our results suggest that the best strategy for Barbary macaques is to release two separate social groups, for which extinction risks remain low ($<5\%$ in the absence of catastrophic events) as long as survival suffers minimal release costs. Sensitivity testing showed that extinction risks are more sensitive to changes in release costs on survival than on reproduction, and that sensitivity to initial sex ratio depends on initial group size. Extinction risk is dramatically affected by catastrophic events, although it is not highly sensitive to variations in the probability of occurrence of such events. Reinforcement releases help counter the effects of high release costs on survival, thus considerably improving probabilities of population persistence. Our model presents highly promising prospects for the successful reintroduction of a Barbary macaque population, and for the conservation of this species, which is the only extant nonhuman primate in North Africa.

RÉSUMÉ

Les analyses démographiques fournissent des informations précieuses pouvant grandement améliorer la planification et la prise de décision en matière de réintroduction, contribuant ainsi à augmenter les chances de succès. Nous avons développé un modèle pour évaluer les chances de succès d'une réintroduction de primate en danger d'extinction, le magot (*Macaca sylvanus*). Le modèle

---

Nelly Ménard and Pascaline Le Gouar should be considered joint senior author.

Animal Conservation, 2025; 0:1–14
https://doi.org/10.1111/acv.70015

intègre des paramètres vitaux âge-spécifiques estimés à partir de 11 ans de données démographiques sur une population sauvage, des réductions de survie et de reproduction dues à de potentiels coûts de réintroduction, de la stochasticité démographique et environnementale, des lâchers de renforcement et des événements catastrophiques. Sur la base des individus disponibles considérés comme les meilleurs candidats pour la réintroduction, nous avons comparé les risques d'extinction selon deux stratégies de réintroduction. Une stratégie implique de relâcher tous les individus en un seul grand groupe social, tandis que l'autre implique de former et de relâcher deux groupes plus petits et séparés. Nos résultats suggèrent que la meilleure stratégie pour les magots est de relâcher deux groupes sociaux distincts, pour lesquels les risques d'extinction restent faibles ($< 5\%$ en l'absence d'évènements catastrophiques) tant que la survie subit des coûts de réintroduction minimes. Les analyses de sensibilité ont montré que les risques d'extinction sont plus sensibles aux variations des coûts de réintroduction sur la survie que sur la reproduction, et que la sensibilité au sex-ratio initial dépend de la taille initiale des groupes. Les risques d'extinction sont très fortement affectés par les évènements catastrophiques, mais ne sont pas particulièrement sensibles aux variations de probabilité d'occurrence de ces évènements. Les lâchers de renforcement permettent de contrer partiellement les coûts de réintroduction élevés sur la survie, améliorant ainsi considérablement les probabilités de persistance de la population. Notre modèle présente des perspectives très prometteuses pour la réintroduction réussie d'une population de magots, et pour la conservation de cette espèce, qui est le seul primate non humain vivant en Afrique du Nord

1 | Introduction

Reintroductions have been a major tool in conservation programs for several decades, carried out with the goal of counteracting the decline of threatened species (Griffith et al. 1989). A reintroduction is the intentional release of organisms in a location within their historical range from which the species had disappeared, which aims to re-establish a viable population (IUCN/SSC 2013). Reintroductions can be vital for species conservation, but they often encounter limited success (Bubac et al. 2019). To maximize success chances for primate reintroductions, releases must be carefully planned, with adequate preparation for released individuals' acclimatization, along with follow-up care after release (IUCN/SSC 2002). It is also helpful to make informed decisions to increase both release and reintroduction success to utilize predictive tools like population viability models incorporating reliable demographic parameters (Converse and Armstrong 2016).

Population viability models depend greatly on the quality of the input data, and obtaining precise estimates of demographic parameters is particularly challenging for long-lived species such as primates (King et al. 2014). Moreover, such models should integrate release costs, that is, decreases in survival and fertility in the months or years following release (Sarrazin and Legendre 2000). This phenomenon is linked to various factors, making it hard to anticipate: direct stress related to transport (anesthesia, human contact, disorientation; Tutin et al. 2001), lack of environmental knowledge (food and shelter location and abundance; Sarrazin and Legendre 2000), missing skills due to captivity (food and shelter search, predator avoidance), or the absence of local genetic adaptations (Tutin et al. 2001). Those release costs are a major factor to consider, as reintroduced populations are often based on small numbers of released founders, making any decrease in survival or reproduction potentially significant for population viability. To minimize those release costs, reintroduction programs typically implement an onsite acclimatization phase before release, consisting of a progressive release in several steps, including prerelease animal care and rehabilitation, and post release care and food supplementation (King et al. 2012; Tutin et al. 2001). Modeling population viability prior to reintroduction, integrating potential release costs, allows for predicting population losses and for identifying which group compositions and sizes might be optimal for reintroduction success (Sarrazin and Legendre 2000).

Barbary macaques (*Macaca sylvanus*) are forest-dwelling group-living primates, inhabiting mainly temperate, mountainous areas in Morocco and Algeria (Taub 1977). The cedar-oak forests of the Middle Atlas Mountains in Morocco host about 75% of Barbary macaque wild populations. However, Barbary macaque numbers in this region have decreased from 15,000 to 5000 individuals in 30 years (Ménard, Foulquier, et al. 2014). Since 2008, the species is classified as endangered on the IUCN Red List (Wallis et al. 2020). Its decline is attributed mainly to forest degradation due to overgrazing and inadequate forest management (Camperio-Ciani et al. 2005; Mehlman 1989; Ménard, Foulquier, et al. 2014), and the harvest of young individuals for the illegal pet trade (van Lavieren 2008). Current natural populations are strongly fragmented, with reduced gene flow and significant genetic differentiation (Le Gouar et al. 2021). In 2012, a National Action Plan for the Conservation of Barbary Macaques in Morocco included increasing law enforcement efforts to fight the illegal trade. The success of these efforts has resulted in a steep rise in confiscated individuals from the Moroccan trade markets in recent years (Wallis et al. 2020). As this growing stock of rescued individuals provides candidates for release, Moroccan authorities initiated a reintroduction program which aims to: (1) establish a viable population and bring back the species into an area which Barbary macaques could not recolonize on their own considering their dispersing capabilities and the fragmentation of their habitats (Le Gouar et al. 2021); (2) mitigate the potential reduction or loss of wild populations by establishing an additional one; (3) increase the number of individuals in the wild, with a projected population size comparable to the largest currently viable populations in Morocco; and (4) reinstate a flagship species into the functioning of one of its natural habitats from which it has disappeared.

We developed a population viability model integrating potential release costs to inform decisions for the release of individuals fit for release into the wild. We estimated the risk of extinction of the proposed reintroduced population depending on two release strategies for an initial pool of individuals, either reintroducing all available best candidates as a single social group or releasing sequentially two smaller social groups. In primate reintroduction programs, when released social groups are comprised of captive individuals, they are generally constituted based on various constraints, in particular the need for strong interindividual social bonds and the diminishing acclimatization capacity of captive individuals to wild conditions as they get older (Goldenberg et al. 2019; Shier 2016). These constraints commonly result in group compositions which differ from those of wild groups by typically smaller group size and different age-sex structures (Converse and Armstrong 2016). We investigated the effects of those constraints on reintroduction success by comparing, for each strategy, the extinction risks of released groups with those of groups with standard wild compositions. Our analyses are based on demographic parameters (survival and reproductive rates) derived from 11 years of data on a wild population of Barbary macaques living in Algeria (Neves, Vallet, Cherkaoui, et al. 2023), and the number and age-sex classes of the available captive individuals considered as best candidates for release. Despite the known strong negative effects that release costs may have on the demography of reintroduced populations (Sarrazin and Legendre 2000), those costs are seldom accounted for in population viability models. In our model, we integrate a range of potential release costs estimated from the literature. Our model also incorporates demographic and environmental stochasticity, as well as scenarios incorporating reinforcement releases and potential catastrophic events.

2 | Methods

2.1 | Study Species

Barbary macaques live in large, stable, and cohesive multimale, multifemale groups, generally comprising as many males as females, and as many immatures as adults (Ménard and Vallet 1996). They are polygynandrous and have a highly seasonal reproduction, with a mating period in November–December, followed by a birth period in May–June, after a 5.5-month gestation period (Ménard and Vallet 1993a). Females are philopatric, while males can disperse from their natal group at as early as 3 years old and may disperse to a new group several times in their lifetime (Ménard and Vallet 1993a).

2.2 | Reintroduction Site

Tazekka National Park was chosen as a suitable reintroduction area. The park is located in North-eastern Morocco and stretches over 140 km^2, most of which is covered with cedar-oak forest. The park was part of the Barbary macaque's historical range until they disappeared from the area in 1930, likely because of the advanced degradation state of the forest. Since its creation in 1950, the management plan of the park focuses on restoring the natural ecosystem, which includes reestablishing native plant and animal species. In 2019, NM and PLG conducted an assessment of the habitat in a 530 km^2 area, including the entire park and surrounding forests (*Unpub. data*). Overall, 124.8 km^2 were considered favorable to the establishment of a Barbary macaque population, providing sufficient resources for about 3000 individuals based on densities in other favorable cedar-oak (Ménard, Rantier, et al. 2014) or pure mature oak (Fa 1984) forests.

2.3 | Release Stock and Strategies

Release candidates were poached as infants or juveniles and then illegally detained until they were confiscated in the past 5 years and placed in either one of two Moroccan zoos: Rabat zoo and Dream village. Health and behavioral assessments of individuals in specific age-sex classes were conducted in the zoos to identify those potentially fit for release. Health assessments included virology, parasitology, and bacteriology screenings, while behavioral evaluations ensured that individuals exhibited no abnormal behaviors such as stereotypies or excessive aggression. To ensure successful acclimatization to wild conditions, candidates were limited to those 12 years old or younger, as adaptation becomes increasingly challenging as captive individuals get older (Shier 2016). Moreover, because interactions between unfamiliar fully grown males (≥ 10 years-old) are potentially highly aggressive and can harm their lives and group cohesion, as is known in other macaques (Southwick 1967), each release group was limited to a single fully grown male. A pool of 25 individuals was considered fit for release and moved to the prerelease facilities in Tazekka NP in 2022, where they started the acclimatization process in parties of 2–4 individuals in small enclosures. In 2023, they were moved in two large enclosures (0.13 and 0.27 ha) containing natural vegetation, in two groups of 12 and 13 individuals (groups R-A and R-B, respectively, Table 1). The compositions of those groups resulted from pre-established interindividual social bonds, as well as from the pre-mentioned age-sex constraints. As a result, the compositions of those groups, characterized by an age structure biased in favor of young individuals, and a male-biased sex ratio (Table 1), differ from wild group compositions.

Our analyses aimed to determine which of the two potential release strategies has the lowest risks of population extinction: either reintroducing a large group comprising all available candidates (strategy S-1G, group R, Table 1) or reintroducing sequentially two smaller social groups (strategy S-2G, groups R-A and R-B, Table 1). Additionally, to test the potential effects of the release groups' compositions on reintroduction success, we also ran our model with initial group compositions based on wild groups of similar size (wild groups W, W-A and W-B, of 25, 12 and 13 individuals, respectively, Table 1), estimated from censuses made on 13 wild groups in Morocco.

2.4 | Population Modeling

2.4.1 | Release Costs

We considered two different categories of individuals in the model: released individuals (i.e., the captive individuals which were released into the wild) and wild-born individuals (i.e., individuals born from released and subsequent wild-born individuals). We expressed potential costs of release with release coefficients on reproduction (q) and survival (p), following

TABLE 1 | Age-sex compositions of release (R, R-A, R-B) and wild (W, W-A, W-B) groups as included in the models under strategies S-1G (release of one group) and S-2G (release of two groups).

			Release groups			Wild groups		
			Strategy S-1G	Strategy S-2G		Strategy S-1G	Strategy S-2G	
Sex	Stage	Age[b] (years)	Group R	Group R-A	Group R-B	Group W	Group W-A	Group W-B
F	Adult	≥12	0	0	0	4	1	1
		10–11	3	1	2	1	0	0
		4–9	5	2	3	4	3	3
	Subadult	3	1	0	1	1	1	1
	Juvenile	1–2	0	0	0	2	1	1
	Infant	<1	0	0	0	2	0	1
M	Adult	≥12	0	0	0	2	0	0
		10–11	2	1	1	1	1	1
		5–9	11	7	4	3	1	1
	Subadult	3–4	3	1	2	2	2	2
	Juvenile	1–2	0	0	0	1	1	1
	Infant	<1	0	0	0	2	1	1
	Total		25	12	13	25	12	13
Global sex-ratio[a]			0.36	0.25	0.46	0.56	0.50	0.54
Adult sex-ratio[a]			0.38	0.27	0.50	0.60	0.67	0.67

Abbreviations: N_f, number of females; N_{tot}, number of females and males.

[a] The global and adult sex-ratio is given for each group. It is calculated as N_f/N_{tot}.

[b] Age in 2024 (expected year of first release).

Sarrazin and Legendre (2000). At each time step, age-specific reproductive rates were multiplied by q and survival rates by p. A q or p of 1 would not affect the vital rate, thus representing no cost, while a q or p of 0 would reduce the vital rate to 0, thus representing the highest cost. For released individuals, we considered short-term costs on reproduction and survival in the first year after release with coefficients qs and ps, respectively, and long-term costs during the rest of the individuals' lifespans with coefficients ql and pl, respectively. We considered no release costs for wild-born individuals. We estimated release costs from a literature review of studies reporting on the release success of primate species in similar conditions, that is, group-living species with all or most released individuals coming from captive stocks with little or no experience in the wild, where both prerelease and post release care were provided, including post release veterinary care. We selected four published studies in which survival rates and female reproductive rates after release were provided or could be derived and where causes of death were provided (Table 2). Based on data on individual fate published in those papers, we estimated annual survival and female reproductive rates in the first year after release, in the following years after release, and in all years after release (Table 2). In our calculations of survival rates, we considered individuals which had disappeared from the release site or been definitively returned to captivity as dead because they are no longer part of the studied populations. In our calculations of reproductive rates, we included only live infants and the number of females of reproductive age each year. We then calculated short-term and long-term release costs on female reproduction and global survival, as their rates in the released population divided by their rates in wild populations (Table 2). Based on the minimum, maximum, and intermediate values of those estimated costs, we tested nine different combinations of costs in our models (Table 3).

2.4.2 | Life Cycle

We constructed a post-breeding census, age-classified projection model (Caswell 2001) with a 1-year projection interval and 24 age-classes, from 0 to 23 years old (Figure 1). We estimated the vital rates included in the model from 11 years of demographic data on a wild Barbary macaque population living in Tigounatine (Djurdjura National Park) in Algeria from 1983 to 1993 (Table 4; Neves, Vallet, Cherkaoui, et al. 2023) whose oldest individual died at about 23 years-old. Age-specific female survival rates were estimated in Neves, Vallet, Cherkaoui, et al. (2023) with the Kaplan–Meier method (Kaplan and Meier 1958). Because 100% of the macaques in the Tigounatine

TABLE 2 | Estimated costs of release in four primate release projects.

Species	*N*[a]	1st year[b] *S*[j]; *R*[k]	> 1st year[c] *S*[j]; *R*[k]	Total[d] *S*[j]; *R*[k]	Wild[e] *S*[j]; *R*[k]	*ps*[f]; *qs*[g]	*pl*[h]; *ql*[i]	Causes of death	References
Varecia variegata variegata (black and white ruffed lemur)	13	0.77; 0	0.85; 0.44	0.82; 0.35	0.91[1]; 0.58[2]	0.85; 0	0.93; 0.76	62.5% predation 12.5% malnutrition 12.5% unknown 12.5% re-captured	Britt et al. (2004) [1]Morland (1991) [2]Morland (1990)
Pan troglodytes troglodytes (Chimpanzee)	37	0.81; NA[l]	0.97; 0.29	NA; 0.29	0.95[3]; 0.16–0.22[4]	0.85; NA	1; 1	42.86% disappeared 35.71% fled 14.28% killed by chimpanzees 7.14% drowned	Goossens et al. (2005) [3]Hill et al. (2001) [4]Thompson et al. (2007)
Gorilla gorilla gorilla (Western lowland gorilla)	51	0.98; 0	NA; NA	0.97; 0.20	0.97; 0.18–0.20	1; 0	1; 1	37.5% unknown 25% health issues 25% fights 12.5% drowned	King et al. (2012)
Chlorocebus aethiops (Vervet monkey)	59	0.31; 0.66	NA; NA	NA; NA	0.85; 0.54[5]	0.36; 1	NA; NA	70.73% disappeared 9.76% predation 7.32% unknown 4.88% injured 2.44% snake bite 2.44% killed by humans 2.44% re-captured	Wimberger et al. (2010) [5]Turner et al. (1987)

[a] *N*: number of released individuals.
[b] 1st year: annual rates the first year after release.
[c] > 1st year: mean annual rates for the following years.
[d] Total: mean annual rates in all years.
[e] Wild: annual rates in wild populations.
[f] *ps*: short-term cost on survival (0 = highest cost; 1 = lowest cost).
[g] *qs*: short-term cost on reproduction (0 = highest cost; 1 = lowest cost).
[h] *pl*: long-term cost on survival (0 = highest cost; 1 = lowest cost).
[i] *ql*: long-term cost on reproduction (0 = highest cost; 1 = lowest cost).
[j] *S*: annual survival rate.
[k] *R*: annual reproductive rate.
[l] There were no females of reproductive age the first year.

TABLE 3 | Nine different combinations of release costs tested in the models.

Combinations	*ps*[a]	*pl*[b]	*qs*[c]	*ql*[d]
1	0.36 [max]	0.93 [max]	0 [max]	0.76 [max]
2	0.36 [max]	0.93 [max]	0.5 [int]	0.88 [int]
3	0.36 [max]	0.93 [max]	1 [min]	1 [min]
4	0.68 [int]	0.96 [int]	0 [max]	0.76 [max]
5	0.68 [int]	0.96 [int]	0.5 [int]	0.88 [int]
6	0.68 [int]	0.96 [int]	1 [min]	1 [min]
7	1 [min]	1 [min]	0 [max]	0.76 [max]
8	1 [min]	1 [min]	0.5 [int]	0.88 [int]
9	1 [min]	1 [min]	1 [min]	1 [min]

Note: [max] Maximum costs estimated from the literature. [min] Minimum costs estimated from the literature. [int] Intermediate costs estimated from the literature.

[a] *ps*: short-term cost on survival (0 = highest cost; 1 = lowest cost).

[b] *pl*: long-term cost on survival (0 = highest cost; 1 = lowest cost).

[c] *qs*: short-term cost on reproduction (0 = highest cost; 1 = lowest cost).

[d] *ql*: long-term cost on reproduction (0 = highest cost; 1 = lowest cost).

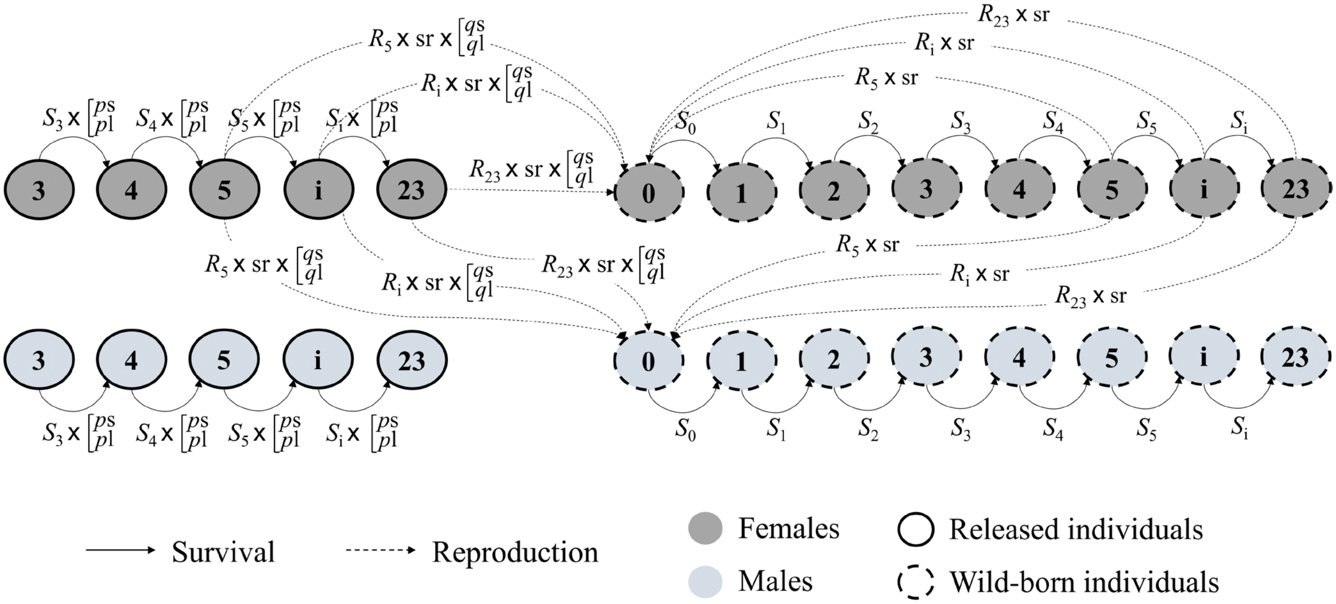

FIGURE 1 | Age-structured life cycle graph of a reintroduced Barbary macaque population with post-breeding census as used in the model. The nodes refer to the different age classes from ages 0 to 23. Dark nodes refer to females and light nodes to males. Solid node outlines refer to released individuals and dashed node outlines to wild-born individuals. The survival transitions are shown with solid lines, and the recruitment transitions with dashed lines. *S*i: Annual survival rate from age *i* to age i_{+1}. *R*i: Annual female reproductive rate at age *i*. *p*s and *q*s: Short-term release costs on survival and reproduction, respectively. *p*l and *q*l: Long-term release costs on survival and reproduction, respectively. *sr*, Sex ratio at birth.

study group were individually identified and censused on each observation day, and because female Barbary macaques are strictly philopatric, all female deaths were known. Males are the dispersing sex. Their disappearances could be ascertained as deaths only if they were found dead, or as emigrations only if they were subsequently observed in other groups. Thus, only the local survival (or apparent survival, that is, the probability that an individual remains within the study population) of males, rather than their true survival, could be estimated. In Barbary macaques, dispersing males always integrate into another social group (Kuester and Paul 1999; Ménard and Vallet 1996). Therefore, because there is currently no Barbary macaque population at the release site, we assumed that males can only disperse into another released group (if several groups are present), and will remain in the global population, or disappear from the population (if only one group is present). Male migrations were thus included in the model by assuming that when several groups are present, male survival rates are similar to female survival rates in the global population, that is, they are not affected by emigration and immigration (Table 4). When only one group is present, we considered the survival rates of males of dispersing age (4–15 years-old) to be similar to the local survival rates of males in the wild Tigounatine population, that is, emigrant males are lost to the population (Table 4). Because Barbary

TABLE 4 | Age-specific estimates of male and female survival and female reproductive rates in a wild population of Barbary macaques (Neves, Vallet, Cherkaoui, et al. 2023).

Age (years)	Female survival rate	Male survival rate (2 groups[a])	Male survival rate (1 group[b])	Female reproductive rate
0	0.82	0.82	0.82	0
1	0.96	0.96	0.96	0
2	0.98	0.98	0.98	0
3	0.97	0.97	0.97	0
4	0.98	0.98	0.75	0
5	0.99	0.99	0.71	0.46
6	0.99	0.99	0.67	0.60
7	0.99	0.99	0.65	0.69
8	0.99	0.99	0.63	0.74
9	0.96	0.96	0.61	0.76
10	0.98	0.98	0.55	0.78
11	0.93	0.93	0.34	0.78
12	0.93	0.93	0.34	0.78
13	0.93	0.93	0.34	0.77
14	0.93	0.93	0.34	0.75
15	0.93	0.93	0.34	0.73
16	0.57	0.57	0.57	0.71
17	0.57	0.57	0.57	0.69
18	0.57	0.57	0.57	0.66
19	0.57	0.57	0.57	0.64
20	0.57	0.57	0.57	0.61
21	0.57	0.57	0.57	0.59
22	0.57	0.57	0.57	0.56
23	0	0	0	0

[a] Male survival rates are similar to females' when two groups are present, i.e., males disperse within the population so that their dispersal does not affect their survival rates.

[b] Survival rates of males aged 4–15 years old are lower when only one group is present to account for the disappearance of dispersing males.

macaques are polygynandrous, paternity cannot be ascertained without genetic analyses. Reproductive rates are thus only available for females (Neves, Vallet, Cherkaoui, et al. 2023). Females become sexually mature at 4 years old, but first conceptions usually occur at 5 years old (Ménard and Vallet 1993a). We considered in the model that females become reproductive at 5 years old (Table 4). Females can produce only one infant per year.

The model's parameters were S_i, the survival rate at age *i* (i.e., the probability of surviving from age *i* to age i_{+1}) and R_i, the female reproductive rate at age *i* (i.e., the number of infants produced alive per year by a female of age *i*). Released individuals of age *i* survive each year with a probability of S_i multiplied by *p*s the first year after release, and by *p*l the following years (Figure 1). Released females aged ≥ 5 years old produce infant wild-born females and males (if at least one male of reproducing age is present) with a probability of *R*i multiplied by the sex-ratio at birth (*sr*; see details on its calculation in Section 2.4.3) and by *q*s the first year after release, and *q*l the following years (Figure 1). Wild-born individuals of age *i* survive each year with a probability of S_i. Wild-born females aged ≥ 5 years old produce infant wild-born females and males (if at least one male of reproducing age is present) with a probability of R_i**sr* (Figure 1).

2.4.3 | Simulations

We included both environmental and demographic stochasticity in the model. For environmental stochasticity, we calculated the standard deviations (SD) of annual reproduction and survival (σq and σp, respectively). Environmental stochasticity was represented by two coefficients, *x* and *y*, representing environmental effects on reproduction and survival, respectively. At each step (i.e., year), those coefficients were drawn from a normal distribution with mean $= 1$ and $\mathrm{SD} = \sigma q$ for reproduction, and $\mathrm{SD} = \sigma p$ for survival. Hence, x and $y > 1$ in good years and < 1 in bad years. In the simulations, recruitment and survival transitions were multiplied at each step by x and y, respectively. In the two-group model (S-2G), each year both groups were affected by the same coefficients x and y. We introduced demographic stochasticity on survival transitions by drawing, at step t_{+1}, the number of individuals N_{i+1} from a binomial distribution of size N_i and probability S_i. We did the same for recruitment transitions by drawing the number of infants N_0 at step t_{+1} from a binomial distribution of size $N\mathrm{f}_{i\geq 5}$ (i.e., the number of females of reproductive age at step t) and probability R_i. To introduce stochasticity on sex ratios at birth, the number of female infants $N\mathrm{f}_0$ was then drawn from a binomial distribution of size N_0 and probability 0.5. The number of infant males $N\mathrm{m}_0$ was then calculated as $N_0 - N\mathrm{f}_0$. Because the goal of the model is to estimate extinction probabilities but not realistic maximum group size, we did not include density dependence in the simulations.

We modeled additional scenarios to explore the effects of reinforcement releases and potential catastrophic events on the population's extinction probabilities. The reinforcement scenario simulated the release of two additional groups into the population, each with a composition identical to group R-B. Based on the expected availability of individuals suitable for release from confiscations from the illegal trade market in the upcoming years, reinforcements were scheduled 5 and 10 years after the initial release. Given that confiscations are expected to decline in the future due to enhanced law enforcement protecting Barbary macaques, we planned no further reinforcement. The catastrophe scenario simulated the effects of severe wildfires. In 2022, Waters and El Harrad (2023) documented a mortality of about 88% in a group of Barbary macaques following a major wildfire in Morocco. Drawing on those observations, and considering an overall mortality of about 20% across all age-sex classes in our Tigounatine population, we applied a 0.15 survival rate multiplier to all age-sex classes during catastrophe years to reach a global mortality of about 88%. In catastrophic years, reproduction rates were set to 0. The probability of catastrophe occurrence was set to 0.033, that is about once every 30 years. In scenarios combining catastrophes and reinforcement releases, if a catastrophe occurred in a planned reinforcement year, then the release was delayed to the following non-catastrophe year.

For each scenario, we ran 1000 simulations of population size trajectories over 50 years (i.e., five times the Barbary macaque generation time; EN, Unpublished data). For S-1G, we calculated extinction probabilities each year as the percentage of trajectories where the group was extinct that year. For S-2G (and for S-1G in scenarios with reinforcement releases), we calculated in the same way the extinction probabilities of each group, and we calculated the extinction probability of the entire population each year as the percentage of trajectories where all groups were extinct that year. We defined a group as being extinct based on three possible non-mutually exclusive conditions: if there were only females remaining, if there were only males remaining, or if there was no adult remaining. The last condition thus assumes that immatures cannot survive and become reproductive without adults. Although this could possibly not be true, it seems likely considering the importance of adults in the protection and stability of the group. The model thus considers the most pessimistic scenario. For all trajectories where a group went extinct, we calculated the percentage of trajectories where they became extinct because of each condition. We performed simulations in R version 4.2.2 (R Core Team 2020).

2.4.4 | Sensitivity Testing

We assessed the sensitivity of extinction risk to variations in input parameters (under scenarios with no reinforcements) by calculating extinction risk's elasticities (i.e., proportional sensitivities) to variations in release costs on survival and reproduction, probability of catastrophe occurrence, and initial sex-ratio in release groups. Minimum and maximum tested values for each parameter are shown in Table 5. Each input parameter varied independently from the others. We calculated the extinction risk's elasticity to each parameter as the percentage of change in extinction risk divided by the percentage of change in the input parameter. We calculated each percentage of change as:

$$\%\,\text{change} = \frac{V_{\max} - V_{\min}}{\left(V_{\max} + V_{\min}\right)/2} \times 100,$$

where $V_{\max}$ and $V_{\min}$ are the maximum and minimum values for either the input parameters or the extinction risk. An elasticity

TABLE 5 | Elasticity of extinction risk to variations in four input parameters (with minimum and maximum values).

	Min–Max	Extinction risk range	Elasticity
Release costs on survival (*ps*, *pl*)[a]	1.0, 1.0–0.36, 0.93	S-1G: 0%–23.8% S-2G: 0.1%–18%	S-1G: 3.95 S-2G: 3.90
Release costs on reproduction (*qs*, *ql*)[a]	1.0, 1.0–0.0, 0.76	S-1G: 0.7%–6.1% S-2G: 0.7%–4%	S-1G: 1.40 S-2G: 1.24
Catastrophe occurrence probability[b]	0.028–0.04	S-1G: 25.6%–42.9% S-2G: 27.1%–45.8%	S-1G: 1.43 S-2G: 1.45
Initial sex-ratio[b,c]	S-1G: 0.36–0.56 S-2G: 0.27–0.5	S-1G: 2.2%–3.1% S-2G: 4.9%–17.4%	S-1G: 0.78 S-2G: 1.88

[a] Under a baseline model with no catastrophes.
[b] Under a baseline model corresponding to the fifth combination of costs (intermediate costs on survival and reproduction) and no catastrophes.
[c] Compares groups R and W for S-1G and groups R-A and W-A for S-2G. For S-2G, extinction risks are those per group, not per the entire population.

ratio close to 1 indicates that the observed change in extinction risk is proportional to the change in the input parameter. A ratio greater than 1 indicates that extinction risk is more sensitive to variations in the parameter than expected, while a ratio less than 1 indicates a lower-than-expected sensitivity.

3 | Results

3.1 | Extinction Probabilities

As expected, whatever the release strategy, extinction probabilities decreased with decreasing release costs (Figure 2, see also details in Appendix S1: Table S1). The population's extinction probabilities were generally higher when releasing only one large group (S-1G) compared with two smaller groups (S-2G), especially when release costs on survival were maximal. Whatever the release strategy, extinction probabilities were comparable between release and wild group compositions (Figure 2a and Figure S1, Tables S1 and S2). The highest extinction probability for the population under S-1G (43.9%–46.8%) or under S-2G (28.0%–31.1%) was associated with maximum costs on all vital rates (Figure 2a; Table S1). When release costs were high, differences in extinction risks between the two strategies were particularly striking before Year 5 (Figure 2a), as the redundancy of having two groups under S-2G seems to buffer the population from extinction during the critical early years post-release. Whatever the strategy, extinction risks stabilized after Year 20 when release costs were no higher than intermediate on both survival and reproduction, and after Year 30 or 40 when they were higher (Figure 2a), that is, when surviving populations had reached sizes of over 40 individuals (Table S1). Extinction probabilities considerably decreased with the addition of reinforcement releases (14.7% under S-1G and 10.4% under S-2G, Figure 2b, Table S3). In scenarios with reinforcements, extinction risks were always zero before Year 10, as populations could not go extinct until the last reinforcement group was released. In scenarios without reinforcements, the lowest extinction probability (0%) was associated with minimum survival costs and minimum to intermediate (S-1G) or minimum to maximum (S-2G) reproductive costs (Figure 2a, Table A1). When reinforcements were included, extinction probabilities fell to ≤ 0.1% under S-2G even with maximal costs on survival, provided reproductive costs were minimal (Figure 2b, Table S3). Reinforcement releases thus partially offset the impact of release costs on population extinction risk.

When catastrophic events were included in the model with a probability of occurrence once every 30 years ($P_{cata} = 0.033$), extinction probabilities increased dramatically across all combinations of costs and both strategies (Figure 2c,d). Extinction probabilities remained generally slightly higher under S-1G

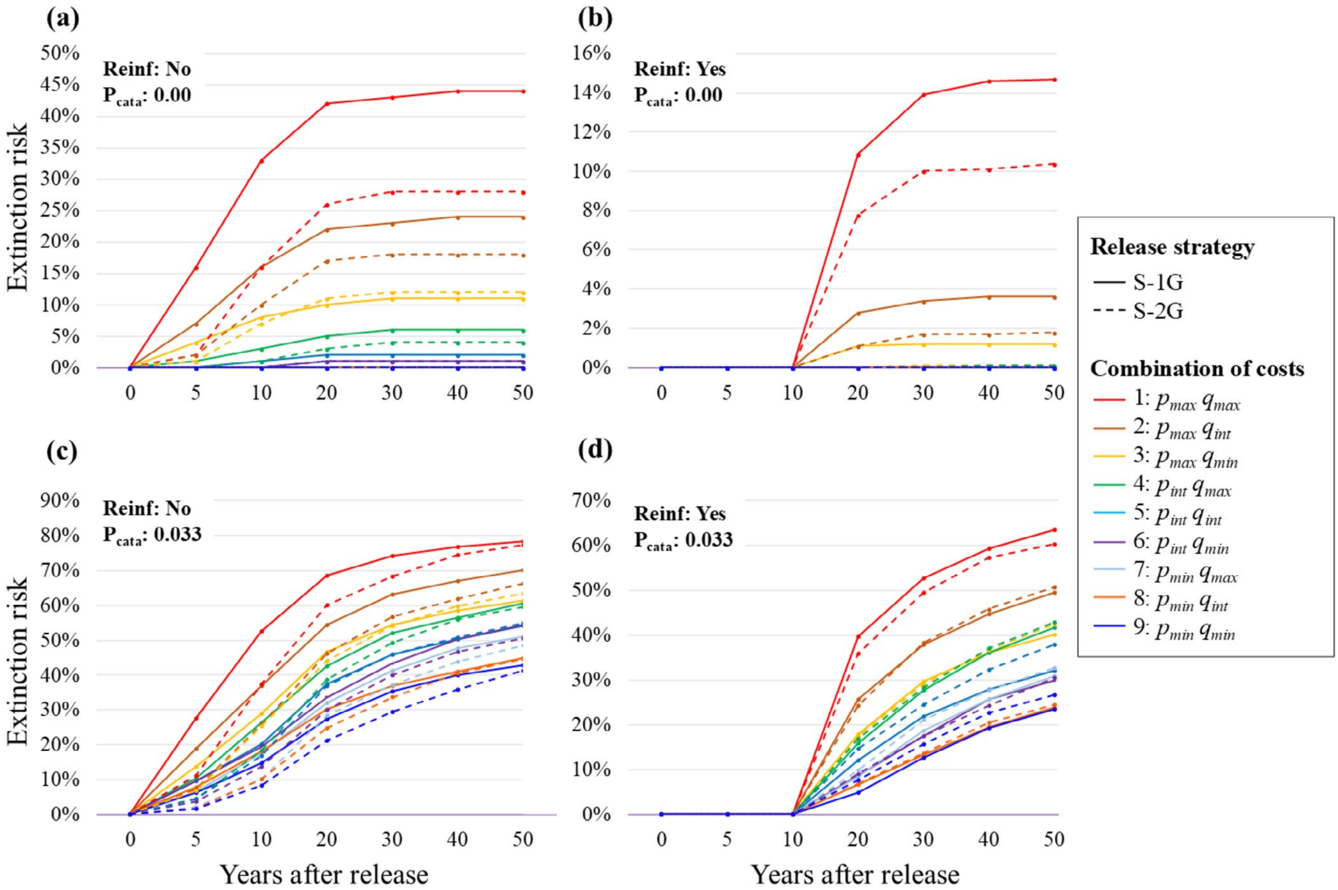

FIGURE 2 | Extinction risks over 50 years of reintroduced populations under strategies S-1G (release of 1 group) and S-2G (release of 2 groups) and 9 combinations of minimum (*min*), maximum (*max*) and intermediate (*int*) short- and long-term release costs on survival (p) and reproduction (q). Reinf: Reinforcements releases at years 5 and 10 (Yes or No); P_{cata}: Probability of occurrence of catastrophic events. Y-axis scales differ across panels to better distinguish the impact of the different release costs among scenarios.

compared to S-2G, with maximum costs resulting in 78.3% under S-1G and 77.2% under S-2G, and minimal costs yielding 42.9% under S-1G and 41.2% under S-2G (Figure 2c, Table S4). The inclusion of reinforcements reduced extinction probabilities, but they remained high even with minimal release costs (Figure 2d, Table S5). Under maximal costs, probabilities dropped to 63.5% for S-1G and 60.4% for S-2G, while minimal costs resulted in 23.5% for S-1G and 26.7% for S-2G (Figure 2d, Table S5). In contrast to scenarios without catastrophes, extinction risks in scenarios with catastrophes did not stabilize during the 50 projected years, regardless of whether reinforcement releases were included or not (Figure 2c,d).

Under a baseline model which assumed intermediate release costs on both survival and reproduction, 18% of population trajectories went extinct within 2 years following a catastrophic event (5% in the first year and 13% in the second). The likelihood of recovery after a catastrophe strongly depended on the population size at the time of the event. Among populations which went extinct within 1 year, the mean and median population sizes during the catastrophic year were 8 and 7 individuals, respectively, compared to 26 and 21 for those that went extinct 2 years after the event. In contrast, among populations which survived at least 5 years after a catastrophe, mean and median population sizes the year of the event were 163 and 99 individuals, respectively.

3.1.1 | Causes of Extinction

In scenarios with no catastrophes and no reinforcement releases, under S-1G, whatever the group composition, the main cause of population extinction was the disappearance of all males in 42%–82% of cases, depending on the release costs (excluding combinations of costs which had ≤ 2 extinct trajectories, Tables S6 and S7). The second most common cause of extinction was the disappearance of all adults from the population (9%–47% of cases). Under S-2G and in the case of release group compositions, the extinction of group R-A was mainly due to the disappearance of all females in 53%–90% of cases (Table S7). For group R-B, it was the disappearance of all males from the group in 36% to 51% of cases, followed by the disappearance of all females from the group in 23%–46% of cases (excluding combinations of costs which had ≤ 2 extinct trajectories). In the case of wild group compositions, extinctions of both groups W-A and W-B were about equally due to the disappearance of females and males for most extinct trajectories (20%–80% of cases depending on the combination of release costs, Table S8).

3.1.2 | Sensitivity Testing

The input parameter for which variations had the greatest impact on extinction risk was release costs on survival, exhibiting an elasticity approximately three times higher than that of release costs on reproduction and probability of occurrence of catastrophic events (Table 5). Extinction risk showed minimal elasticity to variations in the initial sex ratio under strategy S-1G (group size: 25). However, under S-2G (group sizes: 12 and 13), changes in the initial sex ratio influenced the groups' extinction risks considerably more (Table 5).

4 | Discussion

4.1 | Effects of Release Costs on Extinction Risk

We modeled the extinction risks of a reintroduced population of Barbary macaques, testing a range of short-term and long-term potential costs on the survival and reproduction of released individuals. In the absence of catastrophic events, when either one group or two groups were released, the extinction probabilities of the population remained below 5% when release costs on survival were low to moderate, whatever the release costs on reproduction. Although this threshold of 5% may be arbitrary, it has been commonly used in viability analyses as a maximum acceptable extinction risk (Halsey et al. 2015; Kramer-Schadt et al. 2005; Leaper et al. 1999). When reinforcement releases were added to the simulations, extinction probabilities were above that threshold only when release costs on both survival and reproduction were maximal.

The higher sensitivity of extinction risks to release costs on survival compared to costs on reproduction was to be expected considering that in Barbary macaques, as is typically the case in long-lived species, population growth is most influenced by survival rather than by reproduction (Neves, Vallet, Cherkaoui, et al. 2023). Confidence in the model could thus be significantly improved by refining estimates of release costs on survival. Monitoring the initial released groups will provide more accurate estimates of these costs, enabling the model to be refined and applied more reliably to guide strategies for potential reinforcement releases. In the meantime, minimizing release costs on survival appears to be the most critical aspect for increasing success chances. According to our literature review of primate releases, this can be achieved through appropriate prerelease acclimatization and vigilant post-release care. The substantial short-term release costs on survival observed in vervet monkeys in Wimberger et al. (2010) mostly resulted from the disappearance of nearly half of the released individuals, likely due to a lack of group stability. This supports the critical role of adequate prerelease acclimatization, particularly in forming cohesive groups. Similarly, a significant proportion of deaths (36%) among reintroduced chimpanzees resulted from individuals scattering immediately following their release (Goossens et al. 2005). It is thus essential to ensure robust group cohesion during the prerelease phase and to proceed with the release only after confirming the absence of abnormal signs of group instability.

Other factors contributing to mortality in the studied cases included lethal interactions with wild males at the chimpanzee reintroduction site (Goossens et al. 2005) and predation of lemurs by natural predators (Britt et al. 2004). Because wild Barbary macaques are not present at the release site, and because evidence points toward the absence of extant natural predators to the species in Northern Morocco (Bautista et al. 2019; Fa 1986; Mehlman 1989), similar events can be ruled out as potential mortality factors in Tazekka NP. However, domestic and feral dogs have commonly been observed attacking Barbary macaques (Neves, Vallet, Pierre, et al. 2023; Neves et al. 2024). Similar to released lemurs that were more vulnerable to predation by fossas (*Cryptoprocta ferox*) than wild populations (Britt et al. 2004), released Barbary macaques may lack effective antipredator strategies against dogs. However, the macaques have a natural advantage, as unlike fossas, dogs cannot climb trees. This, coupled with the high availability of refuge sites at the release location, should offer some level of protection.

Compared to release costs on survival, costs on reproduction may be more challenging to observe and quantify, especially in long-lived, slow-reproducing species. For example, although overall birth rates of released gorillas were similar to those of wild populations (King et al. 2012), no births were recorded in the first 8 years following the first release. However, Barbary macaques have faster life histories than gorillas, with female first reproductions occurring at around 10 years old in gorillas (King et al. 2012), versus 5 years old in Barbary macaques (Ménard and Vallet 1993a). Generation time for gorillas ranges between 15 and 25 years (Langergraber et al. 2012), as opposed to 10 years for Barbary macaques (EN, unpublished data). The interbirth interval is also longer in gorillas, at about 5 years (King et al. 2012), compared with about 1 year in Barbary macaques (Ménard and Vallet 1996). Given these differences in life history traits, we can expect any post release delays in reproduction to be shorter for Barbary macaques than for gorillas. Moreover, four female Barbary macaques have given birth during the prerelease phase in Tazekka NP, to infants who are still alive. Those prerelease births make us very optimistic for females' ability to successfully produce and raise offspring after release.

4.2 | Effects of Catastrophes on Extinction Risk

Modeled catastrophes had a dramatic impact on extinction risk, even under scenarios with the lowest release costs. For populations to recover from catastrophic events, they must already have high numbers at the time of the event. Extinction risks consistently exceeded the commonly accepted 5% threshold, regardless of release costs. Although the inclusion of reinforcement releases mitigated some of this risk, extinction probabilities still remained above 5%, whatever the release costs. In scenarios without catastrophes, 20–40 years after release, surviving populations had grown sufficiently to be buffered against demographic and environmental stochasticity, allowing extinction risks to stabilize. However, when catastrophes were included, the sudden, severe mortality and reproduction halts caused by these events disrupted population stability. The intensity of such catastrophes appeared to prevent the population from reaching a stable size even 50 years after release, resulting in persistently increasing extinction risk over time. The very high mortality rate applied during catastrophe years was based on observations from a single wild group that experienced significant losses during a wildfire event in Morocco (Waters and El Harrad 2023). However, other groups in the same area suffered fewer fatalities. Our model therefore represents a pessimistic scenario, assuming higher mortality across all groups.

Sensitivity analyses revealed that extinction risk was not highly sensitive to variations in the probability of catastrophic events. However, considering the dramatic effects catastrophes had on the extinction risk, obtaining more accurate estimates for the occurrence of such events would be helpful to enhance the model's reliability. However, this is inherently challenging considering the unpredictable nature of catastrophic events, further complicated by the anticipated effects of climate change. Wildfires are expected to become more severe and frequent globally in the next decades (Pausas and Keeley 2021), and Morocco is particularly vulnerable to droughts, for which severity is projected to increase in the near future (Gumus et al. 2024).

4.3 | Effects of Release Strategy on Extinction Risk

In our simulations, the risks of population extinction were generally lower when releasing two small groups compared with only one larger group, although the magnitude of differences decreased with decreasing release costs. This can be explained by the fact that when only one group is present, its extinction translates into the immediate extinction of the entire population. In contrast, when two groups are present, the population can persist despite the loss of one group. Moreover, our model assumes lower survival rates of males of dispersing age when only one group is released. However, this model assumption is not largely responsible for the variations observed between both strategies. Indeed, when running the same model without reducing the survival of males of dispersing age when only one group is present, extinction risks were globally lower, but the magnitude of differences between both strategies remained similar (Appendix S2). Therefore, the release of two small groups seems to be the most viable strategy for Barbary macaque reintroduction. Beyond the benefits related to population demography, dividing the reintroduction into multiple releases also has operational advantages. Specifically, it allows a first assessment of the animals' adaptation to their new habitat. This preliminary assessment can yield valuable insights that could be employed to refine protocols for future releases, thereby enhancing the chances of a successful reintroduction (Deredec and Courchamp 2007).

Extinction risks were much more sensitive to the released groups' initial sex-ratios in the two-group model (S-2G, 12 and 13 individuals) than in the one-group model (S-1G, 25 individuals). Indeed, under S-1G, when release costs on survival were at their highest, extinction probabilities were consistently lower than those of the smaller group with male-biased sex-ratio under S-2G. In contrast, they were consistently higher than those of the small group with balanced sex-ratio. This shows that the sex-ratio of the population has a greater impact on extinction risk than group size, as the large group released alone is twice the size of each of the two groups released together, with a sex-ratio that falls between the ratios of the two small groups. This is further corroborated by the fact that most extinction events in the small group with male-biased sex-ratio were attributable to the loss of females, whereas those of the small group with balanced sex-ratio were about equally caused by the disappearance of males and females. When releasing only one large group, the primary cause of extinction was the loss of males from the population, due to the model's assumption that dispersing males are lost to the population if there is no available group for them to join. While this is a reasonable assumption, it does highlight a limitation in our model: it does not account for the natural process of group fission. In natural populations, when groups reach a certain size (approximately 80 individuals; Ménard and Vallet 1993b) they fission into smaller groups. In most of our simulations, the groups reached such sizes around 30–40 years after release. Groups persisting and growing to such sizes would undergo fission, thus allowing males to disperse between the resulting groups and to remain within the population. This, however, would be unlikely to affect the model's predictions considering that by the time groups reach such sizes in our simulations, the populations have stabilized and are at very low risk of extinction.

4.3.1 | Effects of Group Composition on Extinction Risk

Surprisingly, whatever the release strategy, we did not find a consistently lower extinction risk for populations with wild group compositions relative to those with release group compositions, except in the case of the small group with a male-biased sex ratio. This group comprised only a quarter of females, that is, three individuals. Such a small number of females makes the group extremely susceptible to demographic stochasticity, frequently resulting in the death of all three females in our simulations, and consequently leading to high extinction risks. The large group with release composition also features an unbalanced sex ratio (36% of females) but this equates to nine females, a number more resilient to demographic stochasticity. The lower extinction risks for the large group with release composition relative to wild composition may be attributed to the generally older age profile of the wild composition. Our model considers the age-specific survival and reproductive rates of individuals, which decline past a certain age threshold of about 16 years old. However, the model does not consider advantages that older individuals, especially females in matrilineal species like the Barbary macaque, might confer on population demography through social learning (Barrett et al. 2017), increasing reproductive success of younger, related females (Alvarez 2000), or maintaining group stability (Sueur et al. 2011), all of which are known to positively influence individual fitness. Given these limitations in our model, we cannot conclude that our proposed group compositions for release are more advantageous than those naturally occurring in the wild.

Our founding population is relatively small, which raises the possibility that inbreeding depression could significantly affect reintroduction success. However, the founding individuals most likely originate from genetically distinct populations, suggesting a high level of genetic diversity. As the degree of admixture within a founding group has been shown to have a greater effect on genetic variation than the number of founders (Biebach and Keller 2012), the risk of inbreeding depression may therefore be limited. Density-dependent effects were excluded from the model, as our primary aim was to assess the likelihood of establishing a viable population rather than to model long-term population regulation. Even under the "best" scenario (incorporating reinforcement releases, no release costs and no catastrophic events) the mean population size 50 years post-release was 1930 individuals (Appendix S1, Table S3), which is below the estimated maximum population size of 3000. While this suggests that density-dependent processes like resource competition may not yet significantly constrain population growth, it is important to recognize that density dependence plays a key role in social dynamics. For instance, Barbary macaque male migration rates are influenced by the number of males and females in a group (Kuester and Paul 1999). Groups with fewer males may experience reduced emigration rates, which can limit genetic exchange, potentially increasing extinction risks. Social dynamics can affect demography in additional ways which were not accounted for in the model. For instance, sociality can affect Allee effects: in highly social species, the Allee threshold can vary depending on group size heterogeneity and intergroup cooperation, which can buffer small populations against extinction (Angulo et al. 2018). Although our model offers valuable insights into extinction risks, integrating such social interdependencies could provide a more nuanced understanding of population dynamics and further refine extinction risk predictions.

5 | Conclusions

Our model presents promising prospects for the successful reintroduction of a Barbary macaque population in Tazekka National Park. The most effective strategy to optimize population demography appears to be the release of two distinct social groups. This approach has the additional advantage of promoting stronger group cohesion by limiting the number of unfamiliar individuals within each group. The most pivotal factor for enhancing the chances of successful reintroduction is to maximize post-release survival. To achieve this, it is imperative to establish strongly cohesive groups prior to release and to monitor individuals closely afterward, providing necessary care as needed. Additionally, subsequent releases, which seem likely considering the number of Barbary macaques being confiscated from the illegal trade market, should considerably help counter the negative effects that potentially high release costs on survival could have on the population. This reintroduction initiative will mark the first soft release of this endangered species. In addition to the important implications it bears for the conservation of the species, it will also allow the rehabilitation of individual Barbary macaques victim to the illegal trade market.

Author Contributions

E.N., N.M. and P.L.G. conceived the ideas and designed the methodology. E.N. led the writing of the manuscript. E.N. and S.L.B. conducted the analyses. N.M., P.L.G., S.L.B., S.I.C., J.I., Z.A., B.I. and L.S. contributed to data acquisition and revised the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgments

Financial support for this study came from the NGO AAP (Animal Advocacy and Protection, Morocco and Netherlands), the French IRP project DIERCOMA from the CNRS (Centre National de la Recherche Scientifique, France). Our study was conducted in close partnership with the "Agence Nationale des Eaux et Forêts", Morocco. We thank the team of the Tazekka National Park and of the NGO AAP who managed the acclimatization phase of the reintroduction project of confiscated Barbary macaques and provided all relevant information about available Barbary macaque candidates and group composition for reintroduction. We thank S. Dunas for completing this information with observations on Barbary macaque behaviors and group cohesion during the acclimatization phase. We thank two anonymous reviewers for their suggestions which greatly improved this manuscript. This is a scientific production of UMR CNRS 6553/OSUR, University of Rennes.

Data Availability Statement

Data available within the article and its Supporting Information.

References

Alvarez, H. P. 2000. "Grandmother Hypothesis and Primate Life Histories." *American Journal of Physical Anthropology* 113, no. 3: 435–450. https://doi.org/10.1002/1096-8644(200011)113:3<435::AID-AJPA11>3.0.CO;2-O.

Angulo, E., G. M. Luque, S. D. Gregory, et al. 2018. "Review: Allee Effects in Social Species." *Journal of Animal Ecology* 87, no. 1: 47–58. https://doi.org/10.1111/1365-2656.12759.

Barrett, B., R. McElreath, and S. Perry. 2017. "Pay-Off-Biased Social Learning Underlies the Diffusion of Novel Extractive Foraging Traditions in a Wild Primate." *Proceedings of the Royal Society B: Biological Sciences* 284, no. 1856: 20170358. https://doi.org/10.1098/rspb.2017.0358.

Bautista, J., S. Castillo, J. L. Paz, J. Llamas, and D. H. Ellis. 2019. "Golden Eagles (*Aquila chrysaetos*) as Potential Predators of Barbary Macaques (*Macaca sylvanus*) in Northern Morocco: Evidences of Predation." *Go-South Bulletin* 15: 172–179.

Biebach, I., and L. F. Keller. 2012. "Genetic Variation Depends More on Admixture Than Number of Founders in Reintroduced Alpine Ibex Populations." *Biological Conservation* 147, no. 1: 197–203. https://doi.org/10.1016/j.biocon.2011.12.034.

Britt, A., C. Welch, and A. Katz. 2004. "Can Small, Isolated Primate Populations Be Effectively Reinforced Through the Release of Individuals From a Captive Population?" *Biological Conservation* 115, no. 2: 319–327. https://doi.org/10.1016/S0006-3207(03)00150-2.

Bubac, C. M., A. C. Johnson, J. A. Fox, and C. I. Cullingham. 2019. "Conservation Translocations and Post-Release Monitoring: Identifying Trends in Failures, Biases, and Challenges From Around the World." *Biological Conservation* 238: 108239. https://doi.org/10.1016/j.biocon.2019.108239.

Camperio-Ciani, A. C., L. Palentini, M. Arahou, L. Martinoli, C. Capiluppi, and M. Mouna. 2005. "Population Decline of *Macaca sylvanus* in the Middle Atlas of Morocco." *Biological Conservation* 121, no. 4: 635–641. https://doi.org/10.1016/j.biocon.2004.06.009.

Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd ed. Sinauer Associates.

Converse, S. J., and D. P. Armstrong. 2016. "Demographic Modeling for Reintroduction Decision-Making." In *Reintroduction of Fish and Wildlife Populations*, edited by D. S. Jachowski, J. J. Millspaugh, P. L. Angermeier, and R. Slotow, 123–146. University of California Press. https://pubs.usgs.gov/publication/70200465.

Deredec, A., and F. Courchamp. 2007. "Importance of the Allee Effect for Reintroductions." *Ecoscience* 14, no. 4: 440–451. https://doi.org/10.2980/1195-6860(2007)14[440:IOTAEF]2.0.CO;2.

Fa, J. E. 1984. "Habitat Distribution and Habitat Preference in Barbary Macaques (*Macaca sylvanus*)." *International Journal of Primatology* 5, no. 3: 273–286. https://doi.org/10.1007/BF02735762.

Fa, J. E. 1986. "On the Ecological Status of the Barbary Macaque *Macaca sylvanus* L. in North Morocco: Habitat Influences Versus Human Impact." *Biological Conservation* 35, no. 3: 215–258. https://doi.org/10.1016/0006-3207(86)90065-0.

Goldenberg, S. Z., M. A. Owen, J. L. Brown, G. Wittemyer, Z. M. Oo, and P. Leimgruber. 2019. "Increasing Conservation Translocation Success by Building Social Functionality in Released Populations." *Global Ecology and Conservation* 18: e00604. https://doi.org/10.1016/j.gecco.2019.e00604.

Goossens, B., J. M. Setchell, E. Tchidongo, et al. 2005. "Survival, Interactions With Conspecifics and Reproduction in 37 Chimpanzees Released Into the Wild." *Biological Conservation* 123, no. 4: 461–475. https://doi.org/10.1016/j.biocon.2005.01.008.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. "Translocation as a Species Conservation Tool: Status and Strategy." *Science* 245, no. 4917: 477–480. https://doi.org/10.1126/science.245.4917.477.

Gumus, V., N. El Moçayd, M. Seker, and M. Seaid. 2024. "Future Projection of Droughts in Morocco and Potential Impact on Agriculture." *Journal of Environmental Management* 367: 122019. https://doi.org/10.1016/j.jenvman.2024.122019.

Halsey, S. J., T. J. Bell, K. McEachern, and N. B. Pavlovic. 2015. "Comparison of Reintroduction and Enhancement Effects on Metapopulation Viability." *Restoration Ecology* 23, no. 4: 375–384. https://doi.org/10.1111/rec.12191.

Hill, K., C. Boesch, J. Goodall, A. Pusey, J. Williams, and R. Wrangham. 2001. "Mortality Rates Among Wild Chimpanzees." *Journal of Human Evolution* 40, no. 5: 437–450. https://doi.org/10.1006/jhev.2001.0469.

IUCN/SSC. 2002. "Guidelines for Nonhuman Primate Re-Introductions." Re-Introduction Specialist Group. https://iucn-ctsg.org/wp-content/uploads/2018/02/Guidelines-for-Nonhuman-Primate-Reintroductions.pdf.

IUCN/SSC. 2013. *Guidelines for Reintroductions and Other Conservation Translocations*. IUCN Species Survival Commission. https://iucn.org/resources/publication/guidelines-reintroductions-and-other-conservation-translocations.

Kaplan, E. L., and P. Meier. 1958. "Nonparametric Estimation From Incomplete Observations." *Journal of the American Statistical Association* 53, no. 282: 457–481. https://doi.org/10.1080/01621459.1958.10501452.

King, T., C. Chamberlan, and A. Courage. 2012. "Assessing Initial Reintroduction Success in Long-Lived Primates by Quantifying Survival, Reproduction, and Dispersal Parameters: Western Lowland Gorillas (*Gorilla gorilla gorilla*) in Congo and Gabon." *International Journal of Primatology* 33, no. 1: 134–149. https://doi.org/10.1007/s10764-011-9563-2.

King, T., C. Chamberlan, and A. Courage. 2014. "Assessing Reintroduction Success in Long-Lived Primates Through Population Viability Analysis: Western Lowland Gorillas *Gorilla Gorilla Gorilla* in Central Africa." *Oryx* 48, no. 2: 294–303. https://doi.org/10.1017/S0030605312001391.

Kramer-Schadt, S., E. Revilla, and T. Wiegand. 2005. "Lynx Reintroductions in Fragmented Landscapes of Germany: Projects With a Future or Misunderstood Wildlife Conservation?" *Biological Conservation* 125, no. 2: 169–182. https://doi.org/10.1016/j.biocon.2005.02.015.

Kuester, J., and A. Paul. 1999. "Male Migration in Barbary Macaques (*Macaca Sylvanus*) at Affenberg Salem." *International Journal of Primatology* 20, no. 1: 85–106. https://doi.org/10.1023/A:1020536317646.

Langergraber, K. E., K. Prüfer, C. Rowney, et al. 2012. "Generation Times in Wild Chimpanzees and Gorillas Suggest Earlier Divergence Times in Great Ape and Human Evolution." *Proceedings of the National Academy of Sciences* 109, no. 39: 15716–15721. https://doi.org/10.1073/pnas.1211740109.

Le Gouar, P., D. Vallet, A. Ernoult, et al. 2021. "A Multiscale Analysis of Landscape Resistance Reveals Genetic Isolates in an Endangered Forest-Specialist Species the Barbary Macaque (*Macaca sylvanus*)." *Biological Conservation* 263: 109337. https://doi.org/10.1016/j.biocon.2021.109337.

Leaper, R., G. Massei, M. L. Gorman, and R. Aspinall. 1999. "The Feasibility of Reintroducing Wild Boar (*Sus scrofa*) to Scotland." *Mammal Review* 29, no. 4: 239–258. https://doi.org/10.1046/j.1365-2907.1999.2940239.x.

Mehlman, P. T. 1989. "Comparative Density, Demography, and Ranging Behavior of Barbary Macaques (*Macaca sylvanus*) in Marginal and Prime Conifer Habitats." *International Journal of Primatology* 10, no. 4: 269–292. https://doi.org/10.1007/BF02737418.

Ménard, N., A. Foulquier, D. Vallet, M. Qarro, P. Le Gouar, and J.-S. Pierre. 2014. "How Tourism and Pastoralism Influence Population Demographic Changes in a Threatened Large Mammal Species."

Animal Conservation 17, no. 2: 115–124. https://doi.org/10.1111/acv.12063.

Ménard, N., Y. Rantier, A. Foulquier, et al. 2014. "Impact of Human Pressure and Forest Fragmentation on the Endangered Barbary Macaque *Macaca sylvanus* in the Middle Atlas of Morocco." *Oryx* 48, no. 2: 276–284. https://doi.org/10.1017/S0030605312000312.

Ménard, N., and D. Vallet. 1993a. "Population Dynamics of *Macaca sylvanus* in Algeria: An 8-Year Study." *American Journal of Primatology* 30, no. 2: 101–118. https://doi.org/10.1002/ajp.1350300203.

Ménard, N., and D. Vallet. 1993b. "Dynamics of Fission in a Wild Barbary Macaque Group (*Macaca sylvanus*)." *International Journal of Primatology* 14, no. 3: 479–500. https://doi.org/10.1007/BF02192778.

Ménard, N., and D. Vallet. 1996. "Demography and Ecology of Barbary Macaques (*Macaca Sylvanus*) in Two Different Habitats." In *Evolutionary Ecology and Behaviour of Macaques*, edited by J. E. Fa and D. G. Lindburg, 106–131. Cambridge University Press.

Morland, H. S. 1990. "Parental Behavior and Infant Development in Ruffed Lemurs (*Varecia variegata*) in a Northeast Madagascar Rain Forest." *American Journal of Primatology* 20, no. 4: 253–265. https://doi.org/10.1002/ajp.1350200402.

Morland, H. S. 1991. "Preliminary Report on the Social Organization of Ruffed Lemurs (*Varecia variegata variegata*) in a Northeast Madagascar Rain Forest." *Folia Primatologica* 56, no. 3: 157–161. https://doi.org/10.1159/000156540.

Neves, E., D. Vallet, S. I. Cherkaoui, et al. 2023. "Behavioral Adjustments of Endangered Barbary Macaques (*Macaca sylvanus*) Living at the Edge of an Agricultural Landscape in Morocco." *American Journal of Primatology* 85, no. 11: e23545. https://doi.org/10.1002/ajp.23545.

Neves, E., D. Vallet, J.-S. Pierre, H. Thierry, P. Le Gouar, and N. Ménard. 2023. "Influence of Environmental Conditions on Population Growth and Age-Specific Vital Rates of a Long-Lived Primate Species in Two Contrasted Habitats." *Population Ecology* 66, no. 2: 71–85. https://doi.org/10.1002/1438-390X.12164.

Neves, E., S. I. Cherkaoui, Z. Amhaouch, C. Duperron, N. Ménard, and P. Le Gouar. 2024. "Conflicts Between Humans and Endangered Barbary Macaques (*Macaca sylvanus*) at the Edge of an Agricultural Landscape in Morocco." *International Journal of Primatology* 45, no. 4: 860–881. https://doi.org/10.1007/s10764-024-00422-w.

Pausas, J. G., and J. E. Keeley. 2021. "Wildfires and Global Change." *Frontiers in Ecology and the Environment* 19, no. 7: 387–395. https://doi.org/10.1002/fee.2359.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/.

Sarrazin, F., and S. Legendre. 2000. "Demographic Approach to Releasing Adults Versus Young in Reintroductions." *Conservation Biology* 14, no. 2: 488–500. https://doi.org/10.1046/j.1523-1739.2000.97305.x.

Shier, D. 2016. "Manipulating Animal Behavior to Ensure Reintroduction Success." In *Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management*, edited by D. Saltz and O. Berger-Tal, 275–304. Cambridge University Press. https://doi.org/10.1017/CBO9781139627078.014.

Southwick, C. H. 1967. "An Experimental Study of Intragroup Agonistic Behavior in Rhesus Monkeys (*Macaca mulatta*)." *Behaviour* 28, no. 1/2: 182–209. https://doi.org/10.1163/156853967x00235.

Sueur, C., A. Jacobs, F. Amblard, O. Petit, and A. J. King. 2011. "How Can Social Network Analysis Improve the Study of Primate Behavior?" *American Journal of Primatology* 73, no. 8: 703–719. https://doi.org/10.1002/ajp.20915.

Taub, D. M. 1977. "Geographic Distribution and Habitat Diversity of the Barbary Macaque *Macaca sylvanus* L." *Folia Primatologica* 27, no. 2: 108–133. https://doi.org/10.1159/000155781.

Thompson, M. E., J. H. Jones, A. E. Pusey, et al. 2007. "Aging and Fertility Patterns in Wild Chimpanzees Provide Insights Into the Evolution of Menopause." *Current Biology* 17, no. 24: 2150–2156. https://doi.org/10.1016/j.cub.2007.11.033.

Turner, T. R., P. L. Whitten, C. J. Jolly, and J. G. Else. 1987. "Pregnancy Outcome in Free-Ranging Vervet Monkeys (Cercopithecus Aethiops)." *American Journal of Primatology* 12, no. 2: 197–203. https://doi.org/10.1002/ajp.1350120207.

Tutin, C. E. G., M. Ancrenaz, J. Paredes, et al. 2001. "Conservation Biology Framework for the Release of Wild-Born Orphaned Chimpanzees Into the Conkouati Reserve, Congo." *Conservation Biology* 15, no. 5: 1247–1257. https://doi.org/10.1111/j.1523-1739.2001.00046.x.

van Lavieren, E. 2008. "The Illegal Trade in Barbary Macaques From Morocco and Its Impact on the Wild Population." *Traffic Bulletin* 21, no. 3: 123.

Wallis, J., M. E. Benrabah, M. Pilot, B. Majolo, and S. Waters. 2020. "*Macaca sylvanus*. The IUCN Red List of Threatened Species 2020: E. T12561A50043570." https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T12561A50043570.en.

Waters, S., and A. El Harrad. 2023. "Wildfire Kills Endangered Barbary Macaques in Bouhachem Mixed Oak Forest, Morocco." *Oryx* 57, no. 1: 10–11. https://doi.org/10.1017/S0030605322001430.

Wimberger, K., C. T. Downs, and M. R. Perrin. 2010. "Postrelease Success of Two Rehabilitated Vervet Monkey (*Chlorocebus aethiops*) Troops in KwaZulu-Natal, South Africa." *Folia Primatologica* 81, no. 2: 96–108. https://doi.org/10.1159/000314636.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.