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Predicting reintroduction costs for wildlife populations under anthropogenic stress

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Abstract

1. In conservation decision-making, it is important to have information not only on the likely effectiveness of conservation actions, but also on the corresponding costs. Reintroduction of wildlife is a commonly applied 'last resort' conservation measure. However, a quantitative approach to predict the costs of reintroduction for sustaining a wildlife population under the influence of time-varying anthropogenic stress is lacking.
2. Here, we fill this gap by quantifying the costs of reintroduction as a function of exposure to an environmental stressor and the size of the wildlife population to be maintained. Our approach combines quantitative stressor–response relationships for vital rates (reproduction and survival) with a wildlife demographic model to compute the impacts of the stressor on the size of the target population. Subsequently, cost estimates are obtained by quantifying the number of captive-reared individuals needed per year in order to maintain a user-defined population size, given the exposure to the stressor of concern. We applied our approach to calculate the reintroduction costs required to restore a minimum viable population (MVP) of peregrine falcons (*Falco peregrinus*) in California over the period 1970–1994, when the population was exposed to the toxicant dichlorodiphenyldichloroethylene.
3. Assuming a gradual yearly increase of 150% in the availability of captive-reared young, 1,753 captive-reared young were required to restore and maintain a MVP of 238 adults. The corresponding reintroduction costs were in total ~\$3,023,000. Assuming lower reintroduction efforts (in terms of the availability of captive-reared young), the projected reintroduction costs decreased by ~33%. However, the population then reached the minimum viable size only 9 years later, thus reflecting a trade-off between costs and population viability.
4. *Synthesis and applications.* The approach presented in this study ensures an adequate prediction of the costs of maintaining a wildlife population at a user-defined size through reintroduction. It can be applied to any wildlife population in order to obtain the number of individuals and corresponding costs required to sustain a

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population under current and future influence of an anthropogenic stressor. This type of information provides important input for decision-making necessary to conserve biodiversity.

KEYWORDS

biodiversity, California, conservation, DDE, peregrine falcon, pressure, reinforcement, restoration

1 | INTRODUCTION

A key goal in conservation biology is the protection of species to ensure stable and viable populations (Shaffer, 1981). This is challenging given the increasing human impact on the environment (IPBES, 2019). Examples of effective conservation measures include habitat preservation, restoration and expansion, hunting restrictions, controlling pollution and invasive species, corridor establishment, and the translocation of individuals (Hayward, 2011; Seddon, Armstrong, & Maloney, 2007). There are a large number of conservation successes in which one or more of these measures have been used to preserve species populations (Hayward, 2011).

Population reintroduction (defined here as the intentional movement and release of organisms into a historical or existing range of a population of conspecifics) is considered as a 'last resort' measure to preserve populations when in situ conservation measures alone are not sufficient (Canessa, Hunter, McFadden, Marantelli, & McCarthy, 2014; Morrison, 2009; Snyder et al., 1996). However, the costs of population reintroduction tend to be high and the success rates low (Fischer & Lindenmayer, 2000; Jule, Leaver, & Lea, 2008; Snyder et al., 1996). As conservation is set in a context of limited funds and resources, it is important to have information not only on the likely effect of conservation actions, but also on the corresponding costs (Carwardine et al., 2008; Wilson, Carwardine, & Possingham, 2009). Some studies have developed methods to estimate the required resources and/or costs of population reintroduction (e.g. Bode & Brennan, 2011; Canessa et al., 2014; Kissel, Palen, & Govindarajulu, 2017; Morandini & Ferrer, 2017). For example, Canessa et al. (2014) have used population models to optimize the cost-effectiveness of release strategies in the reintroduction programme for the southern corroboree frog (*Pseudophryne corroboree*) in Australia. However, none of the methods developed so far explicitly takes into account the influence of time-varying anthropogenic stress on the population of concern, while this may have important consequences for the reintroduction efforts required hence the corresponding costs.

Here, we fill this gap by quantifying the costs of reintroduction via captive breeding and release (hereafter, 'reintroduction') as a function of exposure to an anthropogenic stressor and the size of the wildlife population to be maintained. Our approach combines quantitative stressor-response relationships for vital rates (reproduction and survival) with a wildlife demographic model. This allows us to compute the impacts of anthropogenic stressors on the size of the population. Subsequently, cost estimates are obtained by quantifying the number of captive-reared individuals to be released per year in order to

maintain a user-defined target population size, given the influence of the anthropogenic stressor of concern. We tested our approach by retrospectively estimating the reintroduction costs associated with sustaining the population of peregrine falcons (*Falco peregrinus*) in California under the influence of dichlorodiphenyldichloroethylene (DDE), which is a metabolite of the pesticide DDT. This population is relatively well-studied, which gives the opportunity to rely on detailed information regarding life stages, vital rates and density-dependent processes (Kauffman, Frick, & Linthicum, 2003; Kauffman, Pollock, & Walton, 2004). Moreover, based on past reintroduction efforts of peregrine falcon populations, quantitative information was available on the restoration costs per individual (MPS, 2018).

2 | MATERIALS AND METHODS

2.1 | Model approach

To obtain the costs of reintroduction for sustaining a wildlife population under anthropogenic stress, we used a matrix modelling approach. Matrix population models simulate the dynamics of a population based on a transition matrix that describes all the transitions between the age or developmental stage classes in which the individuals can be classified based on their fecundity and survival rates (Tuljapurkar & Caswell, 1997). We incorporated the impacts of anthropogenic stressors in the transition matrix via effects on fecundity and/or survival rates, which we quantified based on stressor-response relationships combined with time-varying exposure levels. Hence, the transition matrix was an explicit function of the exposure to the stressor. We then simulated population dynamics over time to predict the size of the population, given the exposure to the anthropogenic stressor of concern. Subsequently, we obtained the number of captive-reared individuals to be released per time step by calculating the difference between the predicted population size and a user-defined target population size. We then computed the corresponding costs by multiplying the required number of captive-reared individuals per time step with the costs of one captive-reared individual.

2.2 | Case study

2.2.1 | DDE exposure concentrations

To illustrate our approach, we model the costs of reintroduction via captive breeding and release as a measure to restore a minimum

viable population (MVP) of peregrine falcons in California after declines due to DDE exposure. In 1970, the peregrine falcon was listed as endangered under the Endangered Species Conservation Act, as response to population declines due to the negative impacts of DDE (Jarman, 1994). Around this time, only one or two breeding pairs of the peregrine falcon population of California remained. This prompted reintroduction efforts starting in the 1970s and continuing well into the 1990s (Jarman, 1994; Schipper, Hendriks, Kauffman, Hendriks, & Huijbregts, 2013). Although DDT was banned in the US in 1972, leading to a gradual decrease in DDE levels in the environment, DDE impacts on the population continued until the early 1990s (Jarman, 1994). Measured DDE concentrations in peregrine falcon eggs in California have been obtained from 1948 to 1950, 1969–1983, 1978–1980 and 1983–1988 by Peakall (1974), Hunt et al. (1986), Peakall et al. (1983) and Jarman et al. (1993), respectively. To obtain year-specific DDE exposure concentrations as required to quantify impacts on the population (see Section 2.2.2), we fitted a regression through the geometric means of the measured DDE concentrations (Table 1). We fitted a quadratic model because this was more parsimonious ($AIC_c = 106.1$) than a third-order polynomial

($AIC_c = 108.7$) or a simple linear trend ($AIC_c = 121.6$). The curve revealed that DDE concentrations in Californian peregrine falcon eggs peaked around 1970 and that eggs contained DDE residues from approximately 1945 until 1994 (Figure 1).

2.2.2 | Population model

To calculate the population-level impacts of historical DDE exposure on peregrine falcons in California, we used a transition matrix based on three life stages commonly distinguished in peregrine falcons: juvenile birds that are <1 year old ('fledglings'), 1-year old subadults, and adults of at least 2 years old (Kauffman et al., 2004; Wootton & Bell, 1992). The matrix was configured based on a post-breeding census in which birds start breeding at the end of their second year, when peregrine falcons typically breed (Kauffman et al., 2004). We did not include density-dependence effects on survival and fecundity, as we did not find evidence for density regulation in the time period in which DDE influenced the population (see Appendix S1). As lethal effects of environmentally representative DDE concentrations on peregrine falcons or other raptors were not reported, we

TABLE 1 Summary of the parameter values for the peregrine falcon case study

Model parameter (unit)	Symbol	Distribution	Values	N ^a	Additional information ^b
Fit of historical DDE trend in time (mg/kg wet weight)	DDE	Gaussian (μ, σ^2)	$(-1.9 \cdot 10^5, 1.2 \cdot 10^9) + (192, 1.3 \cdot 10^3) \cdot \text{Year} - (0.05, 8.3 \cdot 10^{-5}) \cdot \text{Year}^2$	17	Based on measured DDE concentrations in peregrine falcons eggs in California from 1948–1950, 1969–1983, 1978–1980 and 1983–1988 [1]
Survival rate wild juveniles (year ⁻¹) ^c	S_{jw}	Beta (α, β)	(14.8, 24.6)	22	Reference fecundity and survival rates are based on 718 encounter history files from California from 1977 through 1999 [2]. For the reference fecundity only data from 1994 through 1999 were used when DDE contamination in Californian peregrine falcon eggs had decreased to negligible levels (Figure 1)
Survival rate juveniles released from captive breeding (year ⁻¹) ^c	S_{jc}	Beta (α, β)	(7.0, 22.1)		
Survival rate 1-year-old subadults (year ⁻¹) ^c	S_{sa}	Beta (α, β)	(22.8, 3.7)		
Survival rate adults (year ⁻¹) ^c	S_a	Beta (α, β)	(165.8, 27.3)		
Reference fecundity ($n \cdot n^{-1} \cdot \text{year}^{-1}$)	F_r	Gaussian (μ, σ^2)	(0.83, 0.11)		
Median effect concentration of DDE (mg/kg wet weight)	EC_{50}	Gaussian (μ, σ^2)	(8.36, 20.0)	7	Based on reproduction rates of merlins (<i>Falco columbarius</i>) exposed to a DDE [3]
Slope of DDE exposure-response curve	β	Gaussian (μ, σ^2)	(1.26, 0.08)		
Costs of one captive-reared individual (US\$)	US\$	—	2,500	—	Based on the average costs per captive-reared juvenile reported for restoration efforts up to 1989 [4]

^aN is the number of data points on which the distribution parameters are based.

^b[1] = Peakall (1974), Hunt et al. (1986) (assuming 80% water in eggs), Peakall et al. (1983) and Jarman et al. (1993), respectively; [2] = Kauffman et al. (2003); [3] = Fox (1979); [4] = MPS (2018).

^cBeta distributions were obtained by calculating the shape parameters from the mean and standard error reported in the literature. To account for environmental stochasticity in the calculation of the MVP, standard deviations were used instead by multiplying the standard errors with the squared root of the sample size (N).

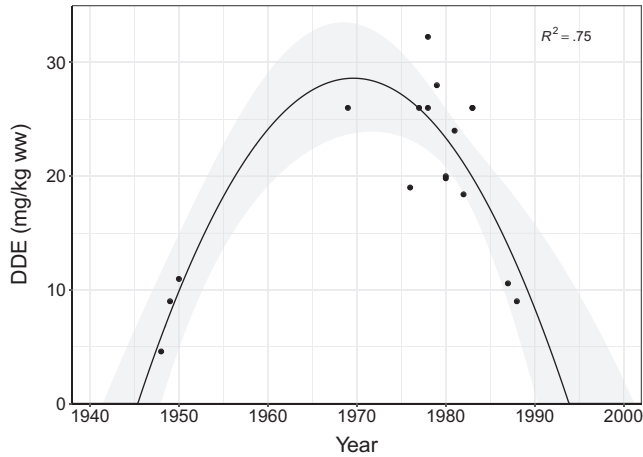


FIGURE 1 Dichlorodiphenyldichloroethylene (DDE) concentrations in Californian peregrine falcon eggs over time, obtained by fitting a quadratic regression (line) through the geometric means (points) of DDE concentrations measured in a given year. The shaded area represents the 95% confidence interval

assumed effects on survival to be negligible and included a fecundity effect only (Schipper et al., 2013). This gives the following transition matrix:

$$M = \begin{bmatrix} 0 & S_{sa}F_{DDE,t} & S_aF_{DDE,t} \\ S_j & 0 & 0 \\ 0 & S_{sa} & S_a \end{bmatrix}, \quad (1)$$

where S_j , S_{sa} and S_a denote the survival rates of juveniles, subadults and adults, respectively. $F_{DDE,t}$ represents the reduced fecundity as function of exposure to DDE at time t , which was modelled according to a log-logistic exposure-response curve (Hendriks & Enserink, 1996):

$$F_{DDE,t} = \frac{F_r}{\left(1 + \left(\frac{C_t}{EC_{50}}\right)^{\frac{1}{\beta}}\right)} \quad (2)$$

where F_r represents the reference fecundity value, i.e. the fecundity under uncontaminated conditions, C_t represents the DDE exposure concentration at time t (see Section 2.2.1), EC_{50} denotes the median effect concentration of DDE, i.e. the concentration resulting in a 50% reduction of the fecundity, and β characterizes the slope of the corresponding exposure-response curve. Because species-specific laboratory data on the influence of DDE on peregrine falcon fecundity were not available, we used toxicity data of DDE impacts on the reproductive success of merlins (*Falco columbarius*) instead (Fox, 1979). Maximum likelihood estimation was used to determine the EC_{50} and slope of the exposure-response curve (Schipper et al., 2013).

We obtained the demographic parameters from published studies that monitored the peregrine falcon population in California from 1977 through 1999 (Kauffman et al., 2003; Schipper et al., 2013).

For the reference fecundity, we only used data from 1994 through 1999 when DDE contamination in Californian peregrine falcon eggs had decreased to negligible levels (Figure 1). Based on a mechanistic bioaccumulation model (Hendriks, Linde, Cornelissen, & Sijm, 2001), it is likely that both wild and captive-reared juveniles have reached equilibrium concentrations of DDE in their body when reaching the breeding stage (see Appendix S2), hence we assumed the same reference fecundity.

To account for uncertainty in the parameters, we randomly sampled 10,000 values from the distributions of the regression parameters of the historical DDE exposure, the parameters of the exposure-response curve (EC_{50} and β) and the demographic parameters (S_j , S_{sa} , S_a and F_r). We assumed beta distributions for the survival parameters (following e.g. McGowan, Runge, & Larson, 2011; Morris & Doak, 2002), and Gaussian distributions for the reference fecundity F_r , the regression parameters of the historical DDE exposure trend and the parameters of the exposure-response curve (Table 1). We accounted for covariation among the slope(s) and intercept of respectively the exposure trend (Figure 1) and the exposure-response curve in the Monte Carlo simulation by correlated sampling of these parameters. The correlation coefficients between the variance of the regression parameters were taken directly from the regression analysis.

2.2.3 | Target population size

As a target for the reintroduction, we used the MVP defined based on an extinction threshold of 50 individuals. We selected this extinction threshold as it is commonly used to account for stochastic effects other than environmental and demographic stochasticity, such as Allee effects and short-term genetic inbreeding (Franklin, 1980; Hilbers et al., 2016). To determine the corresponding MVP, we simulated the dynamics of the population using the transition matrix and varying the initial number of adults until the population had a 95% probability of having at least 50 adults for at least 100 years. The initial number of juveniles and subadults was set equal to 0 individuals. We accounted for demographic stochasticity by sampling the number of offspring per year from a Poisson distribution, and the yearly numbers of subadults and adults from a binomial distribution with their survival rates as probabilities and the simulated number of individuals of the previous year as the number of trials (Akçakaya, 2000; Legendre, Clobert, Møller, Sorci, & Harrison, 1999). Also, we accounted for environmental stochasticity by sampling the 10,000 survival parameters for each year using the standard deviations (instead of the standard errors) to obtain the parameters of the corresponding beta distributions (Table 1; Akçakaya, 2000).

2.2.4 | Reintroduction costs

We obtained the cost estimates based on the number of captive-reared juveniles needed per year in order to reach the MVP (numbers of adult birds) and sustain it over time. The introduced juveniles

were added to the life stage of juveniles in the transition matrix. The number of captive-reared individuals needed per year was then calculated as:

$$N_{j,c,t} = (MVP - N_{a,t+2}) \cdot \frac{1}{S_{jc}S_{sa}}, \quad (3)$$

where $N_{j,c,t}$ and MVP denote the number of captive-reared juveniles per year and the MVP size, respectively, $N_{a,t+2}$ denotes the expected adult population size in two years without reintroduction efforts, S_{jc} denotes the survival of first-year captive reared juveniles (which differs from the survival of wild juveniles; Table 1), and S_{sa} the survival of the 1-year old subadults. We evaluated the adult population N_a 2 years ahead of the introduction efforts because it takes two years before the introduced juveniles become adults. Thus, the juveniles introduced at time t will ensure that the population is sustained at the MVP at time $t + 2$.

We calculated the yearly and cumulative number of captive-reared juveniles to be introduced from 1970 through 1994. In 1970, the peregrine falcon was listed as endangered, the exposure concentrations in California peaked and its peregrine falcon population was reduced to one or two breeding pairs (Herman, 1971; Kauffman et al., 2003; the latter used here as the initial adult population size of the simulations). In 1994, DDE contamination in Californian peregrine falcon eggs had decreased to negligible exposure levels (Figure 1). We simulated an increase in the number of available captive-reared juveniles over time starting from two individuals in 1970 with a yearly increase of 150%, similar to the actual increase in released captive-reared young in the early years of the captive-breeding and release programme in California (Schipper et al., 2013). We applied two additional scenarios with yearly increases of 175% and 125% in the number of available young to represent conservation strategies in which more and less effort, respectively, is undertaken to restore the population. Thus, the number of captive-reared juveniles introduced per year depended on the difference between the MVP and the population size, the survivability of captive-reared juveniles and subadults, and the number of captive-reared juveniles available.

We generated corresponding cost estimates for the three scenarios prospectively as if one lived in 1970. We calculated costs by multiplying the number of captive-reared individuals per year by the costs of one captive-reared individual (Table 1). The unit cost estimate represented the costs of acquiring young peregrine falcons plus hack-site operational costs, including personnel costs to attend hack-sites, falcon food and hack-box construction (Table S1). Each year, we corrected for the expected reduction in the value of capital due to inflation over time by discounting future reintroduction costs to the base year of 1970 using a discount rate of 3%.

2.2.5 | Trade-offs and uncertainty analysis

We explored trade-offs of delaying the reintroduction efforts in order to find a potential optimum where cost effectiveness is

maximized. To this end, we modelled the difference between the MVP and the average number of adults (as a measure of population viability) as a function of the cumulative costs of reintroduction. We gradually decreased the number of years in which captive-reared juveniles were released, starting from 23 years (1970–1992; reintroduction efforts starting immediately), 22 years (1971–1992), ..., until 0 years (no reintroduction efforts), and averaged per run the resulting number of adults and the difference with the MVP over the full 23 year time period. We did this for the default scenario with a yearly increase of 150% in the number of available young.

Finally, we assessed the contributions of uncertainties in the different model parameters to the uncertainty of the cost estimates. To that end, we calculated Spearman rank correlation coefficients between the cost estimates and each of the uncertain parameters based on the 10,000 iterations. The correlation coefficients per year were averaged over the full time period. All analyses were performed in R version 3.3.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Reintroduction costs

Our simulations suggested an MVP of 238 adults. Reaching and sustaining an adult population of this size from 1970 through 1994 required in total 1,753 young birds (~\$3,023,000) based on the default scenario (i.e. a yearly increase of 150% in available young). The number of young birds introduced per year (and hence the costs) increased nonlinearly over time until 1983, with a maximum of 390 individuals (~\$663,000) needed in that year (Figure 2). The projected reintroduction efforts thus peaked at times when DDE concentrations were intermediate (Figure S2). The number of adults exceeded the MVP from 1986 onwards (Figure S3). For a yearly increase of 125% in the number of available captive-reared juveniles, the projected costs were ~33% lower (Figure 2), but the population did not reach the MVP until after 1994 (Figure S3). For the 175% yearly increase scenario, the population reached the MVP in 1983, but the costs increased by ~17% compared to the default scenario. Larger reintroduction efforts thus led to a more rapid recovery of the population, yet at higher costs.

3.2 | Trade-offs between costs and population size

Delaying the reintroduction efforts decreased the total costs required, but also led to greater differences between the MVP and the average number of adults, hence a less viable population (Figure 3). A clear nonlinear relationship was found, indicating that reintroduction paid off mainly when started in the first nine years. Delaying the reintroduction efforts until after 1978 resulted in a lower return on investment, as reflected by the shallower slope of the relationship. The difference between the MVP and the average population size could not be reduced to zero: even with reintroduction starting immediately in 1970, there was a difference of on average approximately

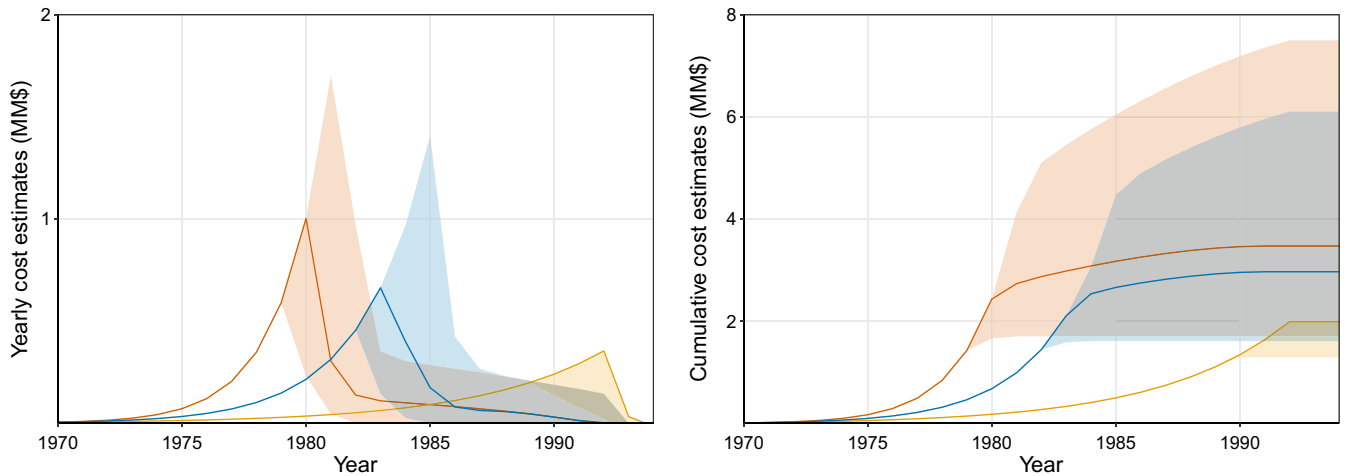


FIGURE 2 Yearly (left) and cumulative (right) cost estimates (MM\$ = millions of dollars) to sustain the population under the influence of dichlorodiphenyldichloroethylene by increasing the adult population to the minimum viable population (238 birds). The blue, red and yellow lines represent cubic spline fits through the medians corresponding with the scenarios of increasing reintroduction efforts of 150%, 175% and 125% each year, respectively, and the shaded areas represent the range between the 5th and the 95th percentiles of the estimates

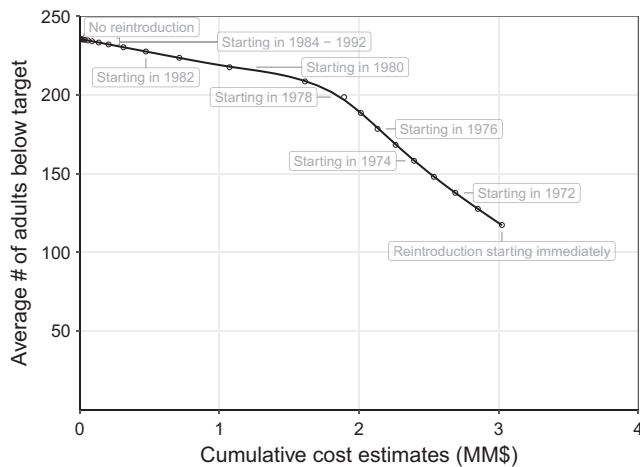


FIGURE 3 The difference between the population target and the average number of adults as a function of the amount of money (MM\$ = millions of dollars) invested to sustain the population under the influence of dichlorodiphenyldichloroethylene by increasing the adult population to the minimum viable population (238 birds). The points represent the medians of 10,000 iterations for each run, the solid line represents the cubic spline fit through these medians and the labels indicate when the reintroduction efforts were started

118 adults with the MVP (Figure 3). This suggests that during the first years of the reintroduction period the availability of young was a limiting factor in reaching the MVP (Figure S3).

3.3 | Uncertainty in reintroduction costs

On average, the uncertainty in the cost estimates was mostly caused by the uncertainty in the survival of the first-year captive reared juveniles (S_{jc}), followed by the uncertainty in adult survival (S_a) and the wild juvenile survival (S_{jw}) and reference fecundity (F_r) (Figure 4). This result was largely consistent across the reintroduction scenarios,

except that the uncertainty in the survival of 1-year-old subadults (S_{sa}) was found to be a major source of uncertainty in the cost estimates specifically in the 125% increase scenario. Correlation coefficients between the survival and fecundity parameters and the cost estimates were all negative: the higher the survival and fecundity the lower the reintroduction costs.

4 | DISCUSSION

4.1 | Peregrine falcon reintroduction in California

We developed an approach to predict wildlife reintroduction costs via captive breeding and release by combining quantitative stressor-response relationships with a wildlife demographic model. To our knowledge, our study is the first to predict the number of individuals and corresponding costs required to sustain a wildlife population at a user-defined size as an explicit and quantitative function of a time-varying anthropogenic stressor. We applied the approach to retrospectively predict the costs of peregrine falcon restoration in California after declines due to DDE exposure. Actual past reintroduction efforts in California were initiated in 1975 with the release of captive-hatched young starting 2 years later (Schipper et al., 2013). The goal was to increase the Californian peregrine falcon population to 120 pairs, which state and federal experts considered sufficient for a self-sustaining population (Jarman, 1994; US Fish & Wildlife Service, 1982). This state-defined target of 120 pairs (240 adults) is almost identical to our estimated MVP of 238 adults, even though in our simulations we may have overestimated the MVP by using standard deviations of demographic parameters that included both sampling variance and true process variance (Akçakaya, 2000; White, Franklin, & Shenk, 2002). Assuming a 150% yearly increase in the number of available young, our calculations suggested that between 1977 and 1992 in total 1,391 young were required to increase the

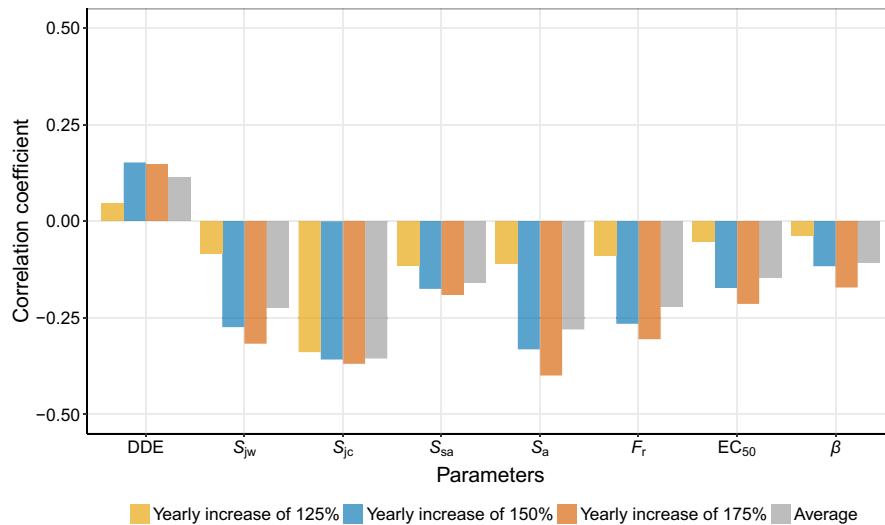


FIGURE 4 Spearman rank correlation coefficients between the yearly cost estimates and each of the model parameters: the historical dichlorodiphenyldichloroethylene (DDE) exposure (DDE), the survival rate of wild juveniles (S_{jw}), the survival rate of captive-reared juveniles (S_{jc}), the survival rate of one-year-old subadults (S_{sa}), the survival rate of adults (S_a), the reference fecundity (F_r) and the parameters of the exposure-response curve (EC_{50} and β). The three scenarios for the reintroduction capabilities (yellow = increasing reintroduction efforts of 125%, blue = increasing reintroduction efforts of 150%, red = increasing reintroduction efforts of 175%) were grouped together to obtain an overall average (grey)

breeding adult population to the MVP in 1993. In reality, between 635 and 777 young were released in California between 1977 and 1992, after which the population recovered to 226 breeding adults in 1992 (Heinrich, 2009; Kauffman et al., 2004; Schipper et al., 2013). This indicates that our model parameters might have been set too pessimistically compared to the actual population dynamics in California between 1977 and 1992, or that the actual past reintroduction efforts were in fact associated with a high risk of failing to reach the target.

4.2 | Cost estimates

We obtained cumulative reintroduction costs by multiplying the number of individuals required with the costs per captive-reared individual. Our results showed that the total costs needed to increase the population to the MVP from 1970 to 1994 were substantial (Figure 2). These cost estimates were associated with uncertainty induced by uncertainties in (a) demographic parameters, (b) historical DDE exposure estimates and (c) the DDE exposure-response curve. For reducing the uncertainty in the costs, our results showed that it is most effective to obtain more survival and fecundity data (Figure 4). Additional uncertainty originates from our unit cost estimate. We estimated the costs of releasing one captive-reared individual based on the captive-breeding and release programme in the Midwest (USA), which differed in some aspects from the reintroduction programme in California. For example, a combination of hacking and (cross-)fostering was used when releasing juveniles in California (Kauffman et al., 2004; Schipper et al., 2013), whereas reintroduction in the Midwest program was based on hacked birds only, which are more expensive (MPS, 2018; see also Table S1). On the other hand, more birds

were released in the Midwest (1,286 in total), which could have lowered the costs per bird. Additionally, the cost estimate based on the Midwest program did not include costs related to transportation, travel to and from breeding and release sites, equipment, infrastructure, overhead and staff time as these were donated free of charge (Patrick Redig, personal communication, August 9, 2018), whereas they are typically incurred in conservation interventions such as reintroduction (Iacona et al., 2018). Due to such differences, the unit costs may have been (slightly) higher or lower in California than in the Midwest. This implies that our total cost estimates are preferably interpreted in a relative way, i.e. comparatively across different reintroduction strategies.

4.3 | Different reintroduction strategies

With a lower availability of captive-reared young, the maximum number of captive-reared juveniles needed per year shifted to later times, when DDE concentrations were lower. This reduced the total number of young to be introduced and the corresponding costs (Figure 2) and emphasizes that reintroduction as a conservation measure is more feasible if employed together with threat abatement or neutralization measures (Griffiths & Pavajeau, 2008; Harding, Griffiths, & Pavajeau, 2016), such as the ban of DDT. Nevertheless, threats such as infectious diseases and climate change are not as easily mitigated (Harding et al., 2016), and delaying reintroduction efforts can greatly increase the risk of population extirpation (Converse, Moore, Folk, & Runge, 2013; Hoffmann et al., 2015). Our results show that without reintroduction efforts, the adult population was predicted to remain well below the MVP (and even well below the threshold of 50 individuals) across the study period (Fig. S3). Reintroduction efforts starting in 1970

ensured that the population reached the MVP within the study period, whereby the target was reached earlier with larger efforts (in terms of the availability in young, and hence investment; Figure S3). Delaying reintroduction efforts led to lower total costs but also to a larger difference between the MVP and the average population size (Figure 3), reflecting a clear trade-off between the costs on the one hand and the risk associated with waiting to reintroduce on the other.

4.4 | Comparison with willingness-to-pay estimates

In biodiversity conservation, willingness-to-pay (WTP) values represent the amount of money individuals are willing to pay for the protection of biodiversity (Loomis & White, 1996; Martín-López, Montes, & Benayas, 2008). WTP values to preserve peregrine falcon populations, expressed as one-time payments, have been estimated at \$8.91 (Kahneman & Ritov, 1994), \$25 (median; Kahneman & Knetsch, 1992), \$25.79 (\$21.83–36.06, 90% confidence interval; Kotchen & Reiling, 2000) and \$29.15 (\$17.00–92.85, 90% confidence interval; Kotchen & Reiling, 1998) per person. After correcting for inflation to the 1970 price level based on the Consumer Price Index (CPI-U from the U.S. Department of Labor's Bureau of Labor Statistics), WTP estimates for the peregrine falcon range between \$2.3 and \$6.9 per person. If we would multiply these estimates by the Californian human population of 18 years and older (13,301,365 individuals in 1970; U.S. Bureau of Census, 1973), the total WTP as a one-time payment to preserve the Californian peregrine falcon population would have been approximately \$31–92 million, assuming that every Californian citizen older than 18 years would contribute equally on average. This greatly exceeds our projections of the cumulative costs to sustain the population under the influence of DDE for all three scenarios. Nevertheless, other anthropogenic stressors affecting the peregrine falcon population, such as habitat loss and climate change, may further increase the costs to sustain the population.

4.5 | Applicability

Given that conservation is challenged by limited funds and resources while biodiversity is becoming increasingly threatened (Butchart et al., 2010; IPBES 2019; Wilson et al., 2009), there is an urgent need to better assess the likely outcomes as well as the costs associated with conservation actions (Carwardine et al., 2008; Wilson et al., 2009). This study provides a straightforward approach to predict the costs of sustaining a wildlife population under anthropogenic stress. It requires a limited number of common ecological variables, like fecundity and survival rates, stressor-response relationships that describe the response of these vital rates to a given environmental stressor, and the unit costs of captive-reared individuals. With these data, the approach can be applied to any wildlife population to prospectively obtain estimates of the number of individuals and corresponding costs required to sustain a population. The reintroduction scenarios employed in

our case study were designed to show how the approach works in practice, yet can be considered relatively simplistic. Future case studies may evaluate more realistic reintroduction scenarios, for example by accounting for fluctuations in the availability of captive-reared individuals or in the unit costs. The approach can be extended to include safeguarding or assisting recovery of individuals from the pressure of concern, in addition to releasing captive-reared individuals. Effectiveness as well as associated trade-offs of a given restoration scenario can be prospectively assessed by identifying when the population size has increased to or above the population target and the stressor has decreased to levels so that conservation measures are not required anymore. Our approach is specifically applicable to wildlife populations that are affected by a clear stoppable threat, which would benefit from reintroduction efforts, where sufficient data are available to develop a population model and where the impact of other anthropogenic stressors affecting the wildlife population is negligible or known. Examples are evaluating the reintroduction costs of (a) lions (*Panthera leo*) after restricting trophy hunting (Creel et al., 2016), (b) African white-backed vultures (*Gyps africanus*) after reducing poison-induced mortality (Monadjem, Kane, Botha, Kelly, & Murn, 2018), or (c) bird species in Guam such as the Mariana Fruit Dove (*Ptilinopus roseicapilla*) after controlling the invasive brown tree snake (*Boiga irregularis*; Rehm, Balsat, Lemoine, & Savidge, 2018). Given that the prediction of these costs will be inherently uncertain and that uncertainty might inflate further when future projections are to be made based on surrogate data or expert-based opinions, the precautionary principle may be applied. The choice of the confidence level then ultimately depends on how precautionary the conservation practitioner wants to and the budget available.

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AUTHORS' CONTRIBUTIONS

J.P.H., M.A.J.H. and A.M.S. designed the methodology; J.P.H. and A.M.S. collected the data; J.P.H. and A.M.S. analysed and interpreted the data; J.P.H., M.A.J.H. and A.M.S. wrote and revised the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data are available from published studies that are referenced in the main text and Table 1.

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REFERENCES

- Akçakaya, H. R. (2000). Population viability analyses with demographically and spatially structured models. *Ecological Bulletins*, 48, 23–38.
- Bode, M., & Brennan, K. E. (2011). Using population viability analysis to guide research and conservation actions for Australia's threatened malleefowl *Leipoa ocellata*. *Oryx*, 45, 513–521. <https://doi.org/10.1017/s0030605311000688>
- Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., ... Watson, R. (2010). Global Biodiversity: Indicators of Recent Declines. *Science*, 328, 1164–1168. <https://doi.org/10.1126/science.1187512>
- Canessa, S., Hunter, D., McFadden, M., Marantelli, G., & McCarthy, M. A. (2014). Optimal release strategies for cost-effective reintroductions. *Journal of Applied Ecology*, 51, 1107–1115. <https://doi.org/10.1111/1365-2664.12253>
- Carwardine, J., Wilson, K. A., Watts, M., Etter, A., Klein, C. J., & Possingham, H. P. (2008). Avoiding costly conservation mistakes: The importance of defining actions and costs in spatial priority setting. *PLoS ONE*, 3, e2586. <https://doi.org/10.1371/journal.pone.0002586>
- Converse, S. J., Moore, C. T., Folk, M. J., & Runge, M. C. (2013). A matter of tradeoffs: Reintroduction as a multiple objective decision. *The Journal of Wildlife Management*, 77, 1145–1156. <https://doi.org/10.1002/jwmg.472>
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Creel, S., M'soka, J., Dröge, E., Rosenblatt, E., Becker, M. S., Matandiko, W., & Simpamba, T. (2016). Assessing the sustainability of African lion trophy hunting, with recommendations for policy. *Ecological Applications*, 26, 2347–2357. <https://doi.org/10.1002/eap.1377>
- Fischer, J., & Lindenmayer, D. B. (2000). An assessment of the published results of animal relocations. *Biological Conservation*, 96, 1–11. [https://doi.org/10.1016/S0006-3207\(00\)00048-3](https://doi.org/10.1016/S0006-3207(00)00048-3)
- Fox, G. A. (1979). A simple method of predicting DDE contamination and reproductive success of populations of DDE-sensitive species. *Journal of Applied Ecology*, 16, 737–741. <https://doi.org/10.2307/2402849>
- Franklin, I. R. (1980). Evolutionary change in small populations. In M. E. Soule & B. A. Wilcox (Eds.), *Conservation biology. An evolutionary-ecological perspective* (pp. 135–150). Sunderland, Massachusetts: Sinauer Associates.
- Griffiths, R. A., & Pavajeau, L. (2008). Captive breeding, reintroduction, and the conservation of amphibians. *Conservation Biology*, 22, 852–861. <https://doi.org/10.1111/j.1523-1739.2008.00967.x>
- IPBES. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. In E. S. Brondizio, J. Settele, S. Díaz, & H. T. Ngo (Eds.), Bonn, Germany: IPBES Secretariat.
- Harding, G., Griffiths, R. A., & Pavajeau, L. (2016). Developments in amphibian captive breeding and reintroduction programs. *Conservation Biology*, 30, 340–349. <https://doi.org/10.1111/cobi.12612>
- Hayward, M. W. (2011). Using the IUCN Red List to determine effective conservation strategies. *Biodiversity and Conservation*, 20, 2563–2573. <https://doi.org/10.1007/s10531-011-0091-3>
- Heinrich, W. (2009). Peregrine falcon recovery in the continental United States, 1974–1999, with notes on related programs of the Peregrine Fund. *Peregrine Falcon Populations in the 21st Century*, 431–444.
- Hendriks, A. J., & Enserink, E. L. (1996). Modelling response of single-species populations to microcontaminants as a function of species size with examples for waterfleas (*Daphnia magna*) and cormorants (*Phalacrocorax carbo*). *Ecological Modelling*, 88, 247–262. [https://doi.org/10.1016/0304-3800\(95\)00111-5](https://doi.org/10.1016/0304-3800(95)00111-5)
- Hendriks, A. J., van der Linde, A., Cornelissen, G., & Sijm, D. T. H. M. (2001). The power of size. 1. Rate constants and equilibrium ratios for accumulation of organic substances related to octanol-water partition ratio and species weight. *Environmental Toxicology and Chemistry*, 20, 1399–1420. <https://doi.org/10.1002/etc.5620200703>
- Herman, S. G. (1971). The peregrine falcon decline in California. II. Breeding status in 1970. *American Birds*, 25, 818–820.
- Hilbers, J. P., Schipper, A. M., Hendriks, A. J., Verones, F., Pereira, H. M., & Huijbregts, M. A. J. (2016). An allometric approach to quantify the extinction vulnerability of birds and mammals. *Ecology*, 97, 615–626. <https://doi.org/10.1890/14-2019.1>
- Hoffmann, M., Duckworth, J. W., Holmes, K., Mallon, D. P., Rodrigues, A. S. L., & Stuart, S. N. (2015). The difference conservation makes to extinction risk of the world's ungulates. *Conservation Biology*, 29, 1303–1313. <https://doi.org/10.1111/cobi.12519>
- Hunt, W. G., Johnson, B. S., Thelander, C. G., Walton, B. J., Risebrough, R. W., Jarman, W. M., ... Walker, W. (1986). Environmental levels of p, p'-DDE indicate multiple sources. *Environmental Toxicology and Chemistry*, 5, 21–27.
- Iacona, G. D., Sutherland, W. J., Mappin, B., Adams, V. M., Armsworth, P. R., Coleshaw, T., ... Possingham, H. P. (2018). Standardized reporting of the costs of management interventions for biodiversity conservation. *Conservation Biology*, 32, 979–988. <https://doi.org/10.1111/cobi.13195>
- Jarman, W. (1994). Levels and trends of DDE in California peregrines. Unpublished report.
- Jarman, W. M., Burns, S. A., Chang, R. R., Stephens, R. D., Norstrom, R. J., Simon, M., & Linthicum, J. (1993). Determination of PCDDs, PCDFs, and PCBs in California peregrine falcons (*Falco peregrinus*) and their eggs. *Environmental Toxicology and Chemistry*, 12, 105–114.
- Jule, K. R., Leaver, L. A., & Lea, S. E. G. (2008). The effects of captive experience on reintroduction survival in carnivores: A review and analysis. *Biological Conservation*, 141, 355–363. <https://doi.org/10.1016/j.biocon.2007.11.007>
- Kahneman, D., & Knetsch, J. L. (1992). Valuing public goods: The purchase of moral satisfaction. *Journal of Environmental Economics and Management*, 22, 57–70. [https://doi.org/10.1016/0095-0696\(92\)90019-5](https://doi.org/10.1016/0095-0696(92)90019-5)
- Kahneman, D., & Ritov, I. (1994). Determinants of stated willingness to pay for public goods: A study in the headline method. *Journal of Risk and Uncertainty*, 9, 5–37. <https://doi.org/10.1007/BF01073401>
- Kauffman, M. J., Frick, W. F., & Linthicum, J. (2003). Estimation of habitat-specific demography and population growth for peregrine falcons in California. *Ecological Applications*, 13, 1802–1816. <https://doi.org/10.1890/01-5324>
- Kauffman, M. J., Pollock, J. F., & Walton, B. (2004). Spatial structure, dispersal, and management of a recovering raptor population. *The American Naturalist*, 164, 582–597. <https://doi.org/10.1086/424763>
- Kissel, A. M., Palen, W. J., & Govindarajulu, P. (2017). A decision-theory approach to cost-effective population supplementation for imperiled species. *Ecological Economics*, 142, 194–202. <https://doi.org/10.1016/j.ecolecon.2017.06.028>

- Kotchen, M. J., & Reiling, S. D. (1998). Estimating and questioning economic values for endangered species: An application and discussion. *Endangered Species Update*, 15, 77–83.
- Kotchen, M. J., & Reiling, S. D. (2000). Environmental attitudes, motivations, and contingent valuation of nonuse values: A case study involving endangered species. *Ecological Economics*, 32, 93–107. [https://doi.org/10.1016/S0921-8009\(99\)00069-5](https://doi.org/10.1016/S0921-8009(99)00069-5)
- Legendre, S., Clobert, J., Møller, A. P., Sorci, G., & Harrison, S. (1999). Demographic stochasticity and social mating system in the process of extinction of small populations: The case of passerines introduced to New Zealand. *The American Naturalist*, 153, 449–463. <https://doi.org/10.1086/303195>
- Loomis, J. B., & White, D. S. (1996). Economic benefits of rare and endangered species: Summary and meta-analysis. *Ecological Economics*, 18, 197–206. [https://doi.org/10.1016/0921-8009\(96\)00029-8](https://doi.org/10.1016/0921-8009(96)00029-8)
- Martín-López, B., Montes, C., & Benayas, J. (2008). Economic valuation of biodiversity conservation: The meaning of numbers. *Conservation Biology*, 22, 624–635. <https://doi.org/10.1111/j.1523-1739.2008.00921.x>
- McGowan, C. P., Runge, M. C., & Larson, M. A. (2011). Incorporating parametric uncertainty into population viability analysis models. *Biological Conservation*, 144, 1400–1408. <https://doi.org/10.1016/j.biocon.2011.01.005>
- Monadjem, A., Kane, A., Botha, A., Kelly, C., & Murn, C. (2018). Spatially explicit poisoning risk affects survival rates of an obligate scavenger. *Scientific Reports*, 8, 4364. <https://doi.org/10.1038/s41598-018-22632-y>
- Morandini, V., & Ferrer, M. (2017). How to plan reintroductions of long-lived birds. *PLoS ONE*, 12, e0174186. <https://doi.org/10.1371/journal.pone.0174186>
- Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology*. Sunderland, Massachusetts, USA: Sinauer.
- Morrison, M. L. (2009). *Restoring wildlife: Ecological concepts and practical applications*. Washington, D.C.: Island Press.
- MPS. (2018). About the falcon restoration project. Retrieved from <http://midwestperegrine.umn.edu/?vw=about>
- Peakal, D. B., Lew, T. S., Springer, A. M., Walker IP, W., Risebrough, R. W., Monk, J. G., ... Kiff, L. F. (1983). Determination of the DDE and PCB contents of peregrine Falcon eggs: A comparison of whole egg measurements and estimates derived from eggshell membranes. *Archives of Environmental Contamination and Toxicology*, 12, 523–528. <https://doi.org/10.1007/BF01056547>
- Peakall, D. B. (1974). DDE: Its presence in peregrine eggs in 1948. *Science*, 183, 673–674. <https://doi.org/10.1126/science.183.4125.673>
- Rehm, E. M., Balsat, M. B., Lemoine, N. P., & Savidge, J. A. (2018). Spatial dynamics of habitat use informs reintroduction efforts in the presence of an invasive predator. *Journal of Applied Ecology*, 55, 1790–1798. <https://doi.org/10.1111/1365-2664.13076>
- Schipper, A. M., Hendriks, H. W. M., Kauffman, M. J., Hendriks, A. J., & Huijbregts, M. A. J. (2013). Modelling interactions of toxicants and density dependence in wildlife populations. *Journal of Applied Ecology*, 50, 1469–1478. <https://doi.org/10.1111/1365-2664.12142>
- Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology*, 21, 303–312. <https://doi.org/10.1111/j.1523-1739.2006.00627.x>
- Shaffer, M. L. (1981). Minimum population sizes for species conservation. *BioScience*, 31, 131–134. <https://doi.org/10.2307/1308256>
- Snyder, N. F., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. B., Toone, W. D., & Miller, B. (1996). Limitations of captive breeding in endangered species recovery. *Conservation Biology*, 10, 338–348. <https://doi.org/10.1046/j.1523-1739.1996.10020338.x>
- Tuljapurkar, S., & Caswell, H. (1997). *Structured-population models in marine, terrestrial, and freshwater systems*. New York: Chapman and Hall.
- U.S. Bureau of Census. (1973). *Census of Population: 1970. Vol. 1: Characteristics of the Population, Part 6: California, Section 2, Table 143*. Washington, DC: U.S. Government Printing Office.
- US Fish and Wildlife Service. (1982). *Pacific coast recovery plan for the American peregrine falcon*. Denver: US Fish and Wildlife Service.
- White, G. C., Franklin, A. B., & Shenk, T. M. (2002). *Estimating parameters of PVA models from data on marked animals* (pp. 169–190). Chicago, Illinois, USA: Population viability analysis. University of Chicago Press.
- Wilson, K. A., Carwardine, J., & Possingham, H. P. (2009). Setting conservation priorities. *Annals of the New York Academy of Sciences*, 1162, 237–264. <https://doi.org/10.1111/j.1749-6632.2009.04149.x>
- Wootton, J. T., & Bell, D. A. (1992). A metapopulation model of the peregrine falcon in California: Viability and management strategies. *Ecological Applications*, 2, 307–321. <https://doi.org/10.2307/1941864>

SUPPORTING INFORMATION

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

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