

September 2014

esa

Volume 24 No. 6

# Ecological

APPLICATIONS

A PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA



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# Assessing predictions of population viability analysis: Peregrine Falcon populations in California

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**Abstract.** Population viability analysis (PVA) has been an important tool for evaluating species extinction risk and alternative management strategies, but there is little information on how well PVA predicts population trajectories following changes in management actions. We tested previously published predictions from a stage-structured PVA of Peregrine Falcons (*Falco peregrinus*) in California, USA (Wootton and Bell 1992), against population trajectories following the 1992 termination of statewide, active management (population supplementation of captive-reared young). In the absence of extensive post-management monitoring, we developed surrogate estimates of breeding population size by calibrating several citizen science data sets (Christmas Bird Count, CBC; and North American Breeding Bird Survey, BBS) to intensive population surveys taken primarily during the active management period. CBC abundance data standardized by observer effort exhibited a strong relationship to intensive survey data ( $r^2 = 0.971$ ), indicated significantly reduced annual population growth rates after management was terminated ( $\lambda = 0.023 \pm 0.013$  SE) than when supplementation occurred ( $\lambda = 0.089 \pm 0.023$  SE), and demonstrated an increasing population as predicted by the PVA. The population trajectory fell within the 95% CI of stochastic simulations of the model either with or without density dependence and assuming either measurement error or process error, but models with process error were most strongly supported by the data. These results indicate that PVA can quantitatively anticipate population trajectories following changes in management, highlight the importance of post-management monitoring of species of concern, and illustrate the benefits of using management changes as large-scale experiments to more rigorously test PVA.

**Key words:** Breeding Bird Survey, BBS; California, USA; Christmas Bird Count, CBC; citizen science; *Falco peregrinus*; management strategy; Peregrine Falcon; population viability analysis, PVA; post-management monitoring; stage-structured matrix model.

## INTRODUCTION

Over the past few decades, quantitative models have become an increasingly important tool in species conservation and evaluation of alternative management plans (Soulé 1986, Beissinger and McCullough 2002, Morris and Doak 2002, Groom et al. 2006, Kareiva and Marvier 2010). Examples of this approach, collectively termed population viability analysis (PVA), include analyses of Spotted Owls (Lande 1988), sea turtles (Crouse et al. 1987), grizzly bears (Doak 1995), sea urchins (Pfister and Bradbury 1996), bats (Frick et al. 2010), and plants (Maschinski et al. 2006). As these models are called upon to generate predictions about the fate of species of concern, an important question is whether their predictions are reliable. Most analyses involve stage-structured matrix models (Caswell 2001), which accommodate a reasonable level of complexity in

variability of population vital rates relative to available data, but which also typically make assumptions that might be violated in real populations, such as an absence of density dependence and the division of individuals within populations into discrete states (Easterling et al. 2000). Hence, information on the predictive ability of these methods is needed, particularly following changes in management that they are used to inform. Such tests can be challenging both because management plans may not incorporate the recommendations of PVAs, and because population monitoring following management is often lacking due to inadequate resources. Therefore, knowledge of the effectiveness of PVAs in predicting the effects of management changes is limited (Brook et al. 2000). Here we report a quantitative assessment of PVA predictions following management change in a species of conservation interest, the Peregrine Falcon (*Falco peregrinus anatum*) in California, USA.

## STUDY SYSTEM AND BACKGROUND

Peregrine Falcons exhibited strong declines throughout their northern hemisphere range from the 1940s to

Manuscript received 10 July 2013; revised 16 December 2013; accepted 23 December 2013. Corresponding Editor: A. K. Brody.

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1960s, coincident with the extensive use of organochlorine pesticides, including DDT (Ratcliffe 1967, Peakall and Kiff 1988). Evidence pointed to pesticide biomagnification as a causal factor, based on high concentrations of DDT's breakdown product, DDE, in falcon tissues and eggs and associated thinning of eggshells, which would often lead to reproductive failure during incubation. Following the banning of DDT use and aggressive implementation of a captive breeding program, Peregrine Falcon populations began to increase throughout North America, although with spatially variable success (Barclay and Cade 1983). In California, falcon populations dropped to very low numbers by the early 1970s (Herman 1971), but were not completely extirpated, and populations began to recover during the 1980s. In light of these population increases, captive breeding in California was scheduled for termination in the early 1990s. Uncertainty about the long-term success of the populations in California remained, however, because of continued high levels of DDE and other pesticide-associated compounds, particularly in the southern portion of the state where pesticide manufacture left high residual pesticide levels in the food web (Venkatesan et al. 1996).

In response to lingering concerns that recovery of the California Peregrine population would reverse following termination of the captive breeding program after the 1992 breeding season, we carried out a PVA to project the expected population trajectory without active management (Wootton and Bell 1992). In light of the spatial difference in contamination and reproductive success in the state, we developed a stage-structured matrix model with spatial structure, and also incorporated density dependence as a hard ceiling for each subpopulation (Appendix A). Although our model was parameterized for Peregrine Falcons, the model framework is broadly applicable to stage-structured species with defined subpopulations. To parameterize the PVA, we took advantage of intensive data that documented size of the breeding population, reproductive success of wild nests, and number of released captives, although we had to use estimates from other populations for rates of survival and movement. Because predicted population dynamics did not match observations over the period of intensive data collection, we subsequently estimated adult survival rates by fitting the model to the population dynamics data, in light of the high sensitivity of model behavior to these rates. These survival estimates were in close agreement with those derived from a subsequent study based on mark-recapture methods (Kauffman et al. 2003). Our conclusions included (1) that the California Peregrine Falcon population exhibited source-sink behavior, (2) that pesticides probably caused population declines by reducing adult survival in addition to their long-appreciated effects on reproductive success, and (3) that the population would continue to grow with the termination of the captive breeding program because excess birds produced in the healthier northern subpop-

ulation would naturally supplement the contaminated southern population. In 1992, the captive breeding program of the Santa Cruz Predatory Bird Research Group (SCPBRG) was terminated. Thereafter, the SCPBRG continued to hack small numbers (typically a half dozen per year) of mostly wild-produced Peregrine nestlings in southern California that were rescued from at-risk urban sites. The subsequent 20-year period now provides an opportunity to test how well our PVA model predicted the trajectory of the Peregrine population in California following this change in its management.

#### METHODS

We compared trajectories of the Peregrine Falcon population in California to stochastic model simulations to assess agreement of predictions with data. Doing this presented a challenge, however, because when the active management ceased, the intensive censusing of the breeding population was also largely curtailed (one systematic census was done in 2006 by the SCPBRG). Following delisting, the United States Fish and Wildlife Service (USFWS) developed a plan to monitor ~10% of the known active nests in California every three years. We are aware of only one year of published data (2003; Green et al. 2006). Because of their limited scope and different methods focused on extant nests, which cannot document population increases, we could not use these data to characterize Peregrine Falcon population dynamics. We therefore had to develop an alternative data series to recreate Peregrine population dynamics. Two volunteer-based data sets documenting bird population dynamics were available to attempt reconstruction: the Breeding Bird Survey (BBS) and the Christmas Bird Count (CBC). The BBS (Robbins et al. 1986) is organized by the USFWS, and depends on a network of trained volunteers that are screened for their bird identification abilities. Data are collected during the summer breeding season along a series of pre-defined routes stratified by geography and habitat. Each route (~40 km long) involves 50 stops at which the observer counts all birds seen and heard over a 3-min period. The CBC (Bock and Root 1981, Butcher et al. 1990) utilizes any person who wishes to participate and involves identifying and counting every individual bird observed over a 24-h period, with observations limited to a circular area 24 km in radius. Counts occur anytime between mid-December and early January; their placement is determined by the presence of interested observers in the area, and to some extent by the variation in habitat available to maximize the number of species recorded. Within these constraints, every attempt is made to keep count locations as consistent as possible once they are established to facilitate abundance comparisons among years. Individuals usually count in groups ("parties") and census effort is estimated as the number of hours each party spends counting birds ("party-hour"). Concerns about the quality of data generated by volunteer-based censuses have been raised (Butcher et al. 1990, Sauer et al. 1994),

but when used with care, CBC and BBS data have been applied usefully to a range of ecological questions (e.g., Wootton 1987, Brown and Maurer 1989, Keitt and Stanley 1997, Hochachka and Dhondt 2000, LaDeau et al. 2007).

We obtained Peregrine Falcon data for California from the BBS through the USFWS, using birds observed per route in each year as an index of abundance (data *available online*).<sup>4</sup> We obtained California CBC data from the online database maintained by the National Audubon Society (2013). We explored two different metrics of these data: the number of falcons per party-hour averaged across all counts, and the proportion of counts recording Peregrine Falcons. The former potentially offers more information about changes in abundance, but might also be affected by counting the same individual multiple times. The latter does not distinguish counts with many observations from those with few observations, and potentially provides limited information when populations are near zero or occupy most available suitable habitat. A priori, we expected that the BBS would perform best and the CBC proportion of routes would perform poorest, based on the degree of standardization, the timing of the intensive censuses (breeding season), and coarseness of the data. We then related each of these abundance indices to the number of falcons counted in the intensive Peregrine Falcon censuses, which were made in the summers of 1980–1993 and in 2006. To try to mitigate seasonal differences between the Christmas Bird Count and the intensive censuses, we used the average of the two CBCs bracketing each intensive (summer) census to derive our population estimate. We chose the index with the highest  $r^2$  value and developed a predictive equation using linear regression from these data, after transforming the data to attain linearity when needed. We used the resulting equation to estimate the falcon population in years lacking detailed censuses to compare against the model predictions. Because we are calibrating these indices explicitly with independent reliable censuses, shortcomings of using volunteer-based data should be minimized. We calculated population growth rates ( $\lambda$ ) as  $\ln(N_{t+1}/N_t)$ , where  $N_t$  is the estimated abundance at time  $t$ .

We carried out a stochastic simulation of our model (Wootton and Bell 1992) in MATLAB version 8.0.0 (MATLAB 2012) to generate predicted population size and 95% confidence intervals. Our original model parameter estimates also included estimates of variability, but the contributions of measurement error vs. stochasticity associated with environmental variation could not be determined because of the diverse sources of information and the lack of procedures in these sources to estimate measurement error. Therefore, we constructed models in which all variability in parameter estimates was either measurement error or environmental variability. In the case of measurement error, we

constructed each run of our simulation by initially drawing a value of each parameter at random from its estimated distribution and then projecting the simulation for 20 years (through 2012). This procedure was repeated 100 000 times and confidence intervals were calculated as the range of values for each year after removing the upper and lower 2.5% of observations. In simulations involving environmental variability, we drew a new estimate for each parameter in each iteration of the simulation, and again repeated each simulation 100 000 times. We simulated cases both with and without the hard density-dependent caps used in our original models to assess their effects on predictions. We compared fits of the predictions to the data by noting whether observations fell within the 95% prediction intervals of the simulations. We also used the simulations to generate a distribution of expected deviances of each annual census by subtracting the value of each simulation point for each year from the yearly median of the simulations, and compared these to the deviances between the median of the simulations and the observed population size in each year. Medians were used rather than means because distributions from the density-dependent model were highly skewed. We grouped the deviances from the simulations into 10 unit bins, and used the proportional frequency in each bin for each year to approximate the probability distribution function under each of the models. We then used the probability of the deviance bin in which the observed population size fell as an index of the likelihood of the model, given the data for a particular year, and used the product of all the yearly values as an overall index of model correspondence. We compared the models by generating evidence ratios for each model, calculated as the ratio of the overall likelihood index of the best-supported model (highest likelihood index) to the likelihood index of the model being compared.

## RESULTS

All three indices correlated positively with the calibration census data, but there were distinct differences in performance (Fig. 1). In contrast to our initial expectations, the BBS fit the data poorly ( $r^2 = 0.144$ ,  $P = 0.18$ ; Fig. 1A), the CBC abundance (square-root of birds per party-hour) fit the data extremely well ( $r^2 = 0.971$ ,  $P < 0.001$ ; Fig. 1B), and the CBC prevalence (proportion of counts with falcons) fit the data remarkably well ( $r^2 = 0.879$ ,  $P < 0.001$ ; Fig. 1C). A conglomerate index with all three variables combined through principle components analysis did not fit better ( $r^2 = 0.786$ ) than the CBC abundance index. Conducting a stepwise regression with all three indices yielded a model with only CBC abundance retained. The 2006 census point potentially exerts high leverage on the relationship. Therefore, we also repeated the analysis after removing this point. The association with CBC abundance was slightly lower ( $r^2 = 0.966$ ). Using the resulting regression equation yielded qualitatively similar results, but as

<sup>4</sup> <https://www.pwrc.usgs.gov/BBS/PublicDataInterface/index.cfm>



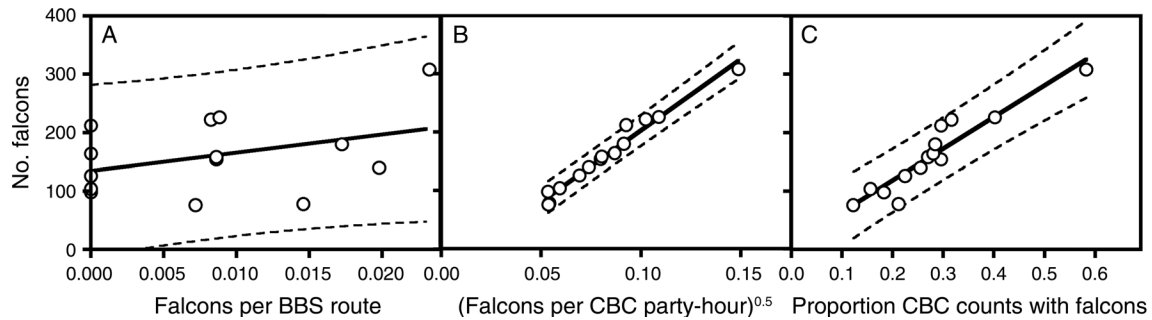


FIG. 1. Ability of different population size metrics derived from citizen science data series to predict Peregrine Falcon (*Falco peregrinus*) abundance from detailed surveys of the California (USA) population (1983–1992, 2006). (A) BBS, Breeding Bird Survey (birds per route); (B) CBC, Christmas Bird Count (birds per party-hour); (C) CBC (proportion of counts with falcons).

population estimates were higher (data not shown), these estimates actually fit all of the models slightly better. In light of the similar behavior, we report the results derived from the full calibration data available, including 2006.

Model simulations (Fig. 2) predicted increasing Peregrine Falcon populations, as in Wootton and Bell (1992) and Kauffman et al. (2004). As expected, terminating captive breeding changed the annual population growth rate, reducing it from  $0.089 \pm 0.023$  (mean  $\pm$  SE) to  $0.023 \pm 0.013$  ( $t$  test,  $P = 0.012$ ). Confidence intervals around the simulated trajectories varied depending on how parameter variability was included in the simulations. Confidence intervals assuming that all variability was the result of measurement error were much wider than when variability was assumed to be the result of environmental fluctuation (Fig. 2). Because parameter estimates were probably affected by both measurement error and environmental fluctuation, reality is probably somewhere in between. The observed population trajectory fell well within the confidence intervals of the predicted trajectories, whether they were generated assuming measurement error or environmental variability, and whether density dependence was included or not. Comparison of the trajectory with the expected (mean) predicted value, however, indicated that all models were somewhat more optimistic than the observations. The trajectory of observed abundance fell outside the 95% confidence interval of model predictions derived by assuming that supplementation of captive-reared birds had continued (Appendix B), indicating that termination of active management had clear effects on the population trajectory that the model was challenged to predict.

Although the observed trajectory fell within the 95% confidence limits of all four models, the relative degree of support among the four models, given the data, varied substantially. Models assuming variability in parameters arising from measurement error were poorly supported compared to models assuming process error variability in parameters (evidence ratios  $>1000$ -fold, Fig. 2). Density-dependent models also tended to be better supported, but the difference in support between

the best-supported model (density dependence with process error) and the density-independent version was small (1.5-fold higher; Fig. 2).

#### DISCUSSION

Our results indicate that PVA can do a very good quantitative job of anticipating population changes in the face of changing management. Our model (Wootton and Bell 1992) predicted that Peregrine Falcons would increase following termination of captive breeding, and our analysis of available data shows that the Peregrine Falcon has indeed been recovering in California over the last two decades. Therefore, while acknowledging that this is a single test, our results suggest that confidence in matrix-based PVA approaches may be merited, and that conservation actions combining organochlorine pesticide bans and captive release appear to have yielded a successful recovery for the Peregrine. There is a lingering concern in these results, however. Field data (Linthicum 1988, 1989, Monk et al. 1989) and our original analysis indicated that the southern subpopulation was still performing poorly in the 1990s, apparently because of high residual concentrations of organochlorine associated with pesticide production. Ideally, we would expect improved performance of the southern subpopulation in recent years because pesticide chemicals are not being added to the environment, and because residual chemicals would be breaking down. The fact that our model predicted well the dynamics over the past two decades suggests that there has been minimal improvement in performance of the southern subpopulation, because we did not incorporate an assumption of improving performance in our model. Therefore further evaluation of Peregrine Falcon productivity in southern California seems warranted.

Most projection matrix-based population models do not include density dependence, on the assumption that it should not be that important at the small population sizes of conservation concern. Although density-independent models performed fairly well, the fact that they consistently overestimated observed population size and performed somewhat more poorly than their density-dependent counterparts suggests that incorporating

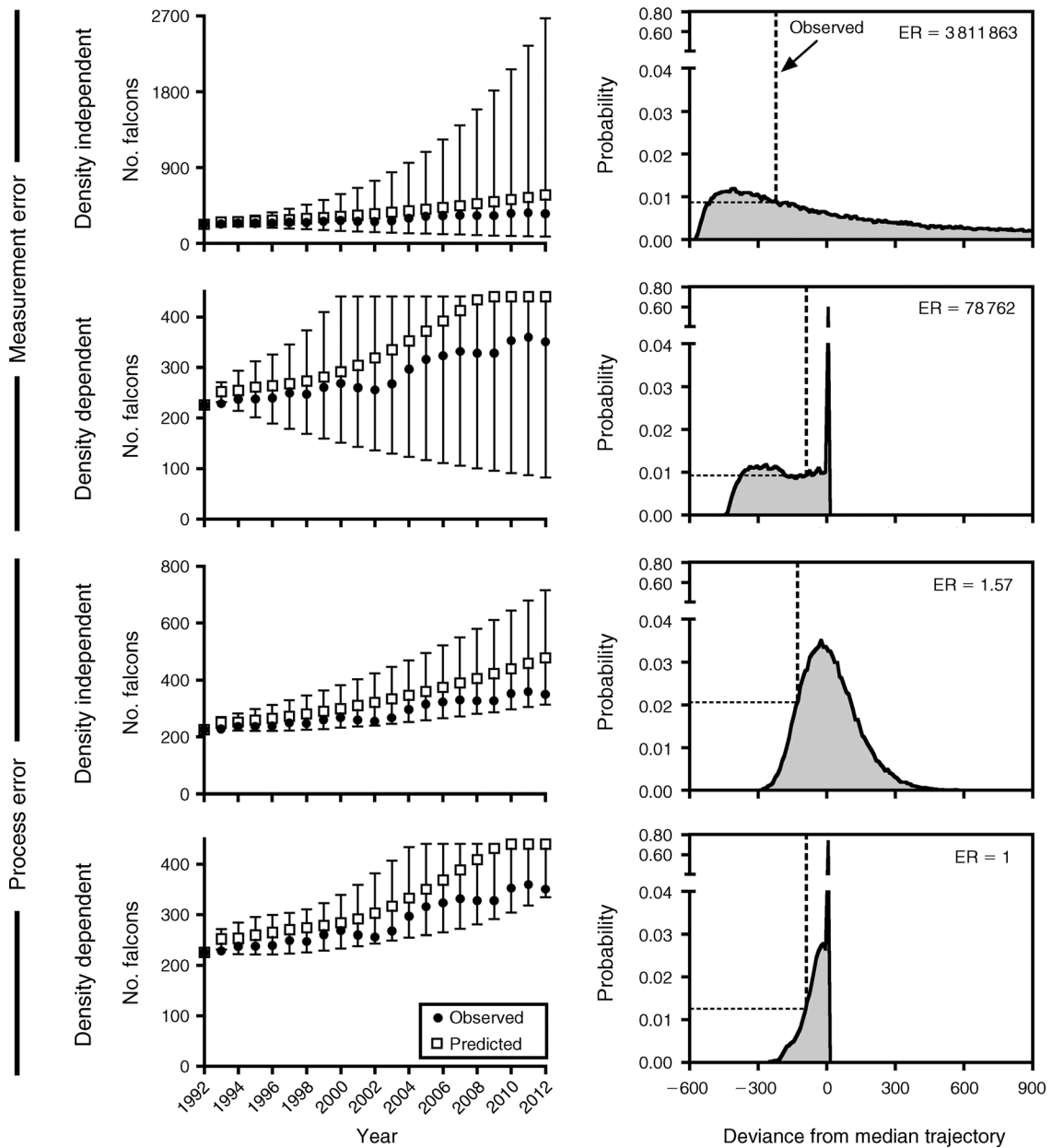


FIG. 2. Comparison of California Peregrine Falcon population size predictions (median with 95% CI) following termination of the captive breeding program in 1992, based on 100 000 simulations of the model of Wootton and Bell (1992) compared to observed population size estimated from the proportion of CBC counts with falcons observed. The left column gives observed and predicted trajectories; note that the y-axis scales vary. The right column shows examples of the probability distribution function (denoted “probability”) of deviance from the median for 2012 based on the 100 000 simulations. The analysis of relative model support derives from the probability distribution functions from all 20 years in the time series, not just 2012. The dashed vertical line indicates observed deviance from the median of the model. The broken horizontal line indicates the corresponding estimated probability of the model, given the data for 2012. Note that the distribution for the density-independent model with measurement error is truncated at the right to allow easier model comparison. ER is the evidence ratio, the relative support for the best model (density-dependent with process error) compared to the model being evaluated.

density dependence may be important to attempt. Our method of adding density dependence was fairly crude because we lacked data to justify a more sophisticated treatment, but it still appeared to help in making successful predictions, so incorporating density depen-

dence might be worthwhile in other analyses. The Peregrine Falcon is considered to exhibit density dependence based in part on nest-site availability (Hunt 1998), and prior analysis demonstrates that density-dependent models better fit Peregrine population dy-

namics in California (Kauffman et al. 2004). Two aspects of our results may suggest that adding density dependence is not critical, however. First, observed trajectories matched those predicted by density-independent models over the first decade of observation. This pattern is perhaps expected, because populations during active management were well below historical levels and density dependence at that point might have been weak, unless the cause of decline was loss of habitat or other resources. At the point at which density dependence became important, the key issue of whether the population would be viable may have been answered. Second, the observed population size did not stray from the confidence intervals of the predicted trajectories of the density-independent models, so consistently underperforming trajectories could arise by chance even if density dependence were not important.

Volunteer-based bird censuses were essential in evaluating the effectiveness of PVA and Peregrine Falcon management outcomes, but alternative metrics performed in a pattern somewhat contrary to our expectations. Our results provide useful lessons for other studies taking advantage of these data resources. Despite their standardization and seasonal correspondence to intensive falcon surveys, BBS counts performed most poorly. Instead, an index based on the abundance of falcons in CBC counts performed best, although it had less standardization and was conducted in winter. The simple proportion of counts detecting falcons in the CBC also did surprisingly well. Several factors probably conspired to produce this result. First, as a formerly endangered bird of prey, Peregrines are relatively rare. The higher standardization of the BBS comes at the expense of having small numbers of observers in the field, so the chances that individual birds will be missed is higher than for more common species, creating more zero observations when the species is in fact present. Second, Peregrines that breed in California are not very migratory (White et al. 2002) so between-season correspondence should be fairly high, although migrants from other areas (Anderson et al. 1988; Golden Gate Raptor Observatory, *unpublished data*) may erode this correspondence to some degree. While these factors will not always be relevant to study species, they are worth considering when designing studies around surveys from citizen scientists. Considering the behavior of multiple indices may be helpful, and having a calibration data set seems particularly valuable.

Population viability analyses can play an important and informative role in species conservation planning, but their reliability needs to be broadly assessed to determine the confidence that we can place in their conclusions. Studies by Brook et al. (2000) on several vertebrates and by Schödelbauerová et al. (2010) on orchids were able to reasonably predict population size in unmanipulated populations 5–28 years beyond model parameterization periods, despite concerns that PVA predictions in general might be unreliable because of

changing conditions, short parameterization windows, and omission of important processes such as density dependence or environmental catastrophes (Coulson et al. 2001, Ellner et al. 2002). These studies did not challenge PVA under manipulated conditions. PVA methods are typically associated with management planning, so a natural opportunity exists to evaluate PVA predictions under new conditions (management implementation). Because the manipulations are known in these circumstances, they provide excellent tests of the approach, particularly when key parameters of the PVA need to be estimated based in prior observations of population dynamics. We were able to test PVAs following management change in this study, but only because relevant ancillary data were available on bird abundance to track changes in Peregrine Falcon populations. More emphasis on post-management data collection and on using management interventions as experiments to test PVA approaches would be beneficial to refine and gain confidence in core quantitative methods underlying conservation biology.

#### ACKNOWLEDGMENTS

We thank the thousands of citizen scientists for their role on collecting the data for the CBC and BBS, K. Dale (National Audubon Society) for assistance in efficiently obtaining some CBC data, and the dedicated staff and volunteers of the Santa Cruz Predatory Bird Research Group, particularly the late B. J. Walton, for their long-term efforts on behalf of the Peregrine Falcon in California. Support was provided in part by the National Science Foundation (DEB 0919420 to J. T. Wootton).

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## SUPPLEMENTAL MATERIAL

### Appendix A

Description of structure and parameterization methods of model presented in Wootton and Bell (1992) ([Ecological Archives A024-074-A1](#)).

### Appendix B

Graphs comparing observed population trajectory of Peregrine Falcons in California and population trajectories predicted if population supplementation of captive breeders had not been terminated ([Ecological Archives A024-074-A2](#)).



**J. Timothy Wootton and Douglas A. Bell. 2014. Assessing predictions of population viability analysis: Peregrine Falcon populations in California. *Ecological Applications* 24:1251–1257. <http://dx.doi.org/10.1890/13-1323.1>**

APPENDIX A. Description of structure and parameterization methods of model presented in Wootton and Bell (1992).

The model was structured as a two-stage (non-breeders and adult breeders) matrix model with two metapopulations and a vector describing population supplementation by captive-reared birds:

$$\begin{bmatrix} F_{n,t+1} \\ N_{n,t+1} \\ F_{s,t+1} \\ N_{s,t+1} \end{bmatrix} = \begin{bmatrix} 0 & y_n b_n & 0 & 0 \\ r_n(1-m) & s_n & r_n m c & 0 \\ \hline 0 & 0 & 0 & y_s b_s \\ r_s m c & 0 & r_s(1-m) & s_s \end{bmatrix} \times \begin{bmatrix} F_{n,t} \\ N_{n,t} \\ F_{s,t} \\ N_{s,t} \end{bmatrix} + \begin{bmatrix} f y_n I \\ 0 \\ (1-f) y_s I \\ 0 \end{bmatrix} \quad (\text{A.1})$$

where  $F_{x,t}$  is the number of non-breeding birds in subpopulation  $x$  ( $n$ -north,  $s$ -south) at time  $t$ ,  $N_{x,t}$  is the number of breeding adults in subpopulation  $x$  at time  $t$ ,  $b_x$  is the annual fledging rate per breeding bird in subpopulation  $x$ ,  $y_x$  is the survival rate of non-breeding birds in subpopulation  $x$ ,  $r_x$  is the rate of survival and recruitment to the breeding population of non-breeding birds in subpopulation  $x$ ,  $s_x$  is the survival rate of breeding birds,  $m$  is the probability that a non-breeding bird moves to a different subpopulation in a year,  $c$  is the probability of surviving movement among subpopulations,  $f$  is the proportion of reared birds released in the northern subpopulation, and  $I$  is the total number of reared birds released. The dashed lines in the matrix of vital rates of free-living birds illustrate how the matrix is subdivided to account for spatial structure:  $2 \times 2$  sub-matrices along the diagonal are the portions of the model describing vital rates of birds that stay within a subpopulation, and off-diagonal sub-matrices describe the fate of birds that move between subpopulations. Note that the variables and birth parameters used here include both males and females to match the population census data used in the paper, rather than the common practice of modeling just females as did Wootton and Bell (1992). To project the population when introductions were terminated, we set  $I = 0$ , which effectively eliminates the vector on the right-hand side of the equation.

The basic model has density-independent vital rates. To introduce density dependence, we placed a hard cap on the number of breeding birds in a subpopulation, reflecting density dependence arising from a limited number of breeding territories ( $T_x$ ). We allowed birds that did not find territories to remain in the population as non-breeding floaters. Hence, when the maximum cap in the northern subpopulation was reached, for example, in the absence of population supplementation the model changes to:

$$\begin{bmatrix} F_{n,t+1} \\ N_{n,t+1} \\ F_{s,t+1} \\ N_{s,t+1} \end{bmatrix} = \begin{bmatrix} 0 & y_n b_n & 0 & 0 \\ r_n(1-m) & s_n & r_n m c & 0 \\ \hline 0 & 0 & 0 & y_s b_s \\ r_s m c & 0 & r_s(1-m) & s_s \end{bmatrix} \times \begin{bmatrix} F_{n,t} \\ N_{n,t} \\ F_{s,t} \\ N_{s,t} \end{bmatrix} + \begin{bmatrix} f y_n I \\ 0 \\ (1-f) y_s I \\ 0 \end{bmatrix} \quad (\text{A.2})$$

where  $d_n$  is the survival rate of floaters.

Details of our methods and data sources for estimating parameters are in Wootton and Bell (1992). Fledging success ( $b_x$ ) and numbers of birds introduced ( $I_x$ ) were estimated from detailed annual nest monitoring data and captive rearing records taken between 1980 and 1992 by the Santa Cruz Predatory Bird Research Group in California. Yearling survival ( $y_x$ ) was taken from studies of peregrine falcons in the United Kingdom, and movement among subpopulations ( $m$ ) was estimated from data on distance between the point of release of introduced female birds and their documented nesting territories for populations in the midwestern United States. Recruitment rate to the breeding population ( $r_x$ ) was estimated using data on rates of recruitment of marked, captive-reared birds to the breeding population in California, and then factoring out the estimated yearling survival. Maximum numbers of territories ( $T_x$ ) were derived from historical records from California. Effects of movement on survival were assumed to be non-existent ( $c = 1$ ) and survival of floaters ( $d_x$ ) was assumed identical to breeding adults ( $s_x$ ). Adult breeder survival was derived by rearranging the model to solve for  $s_n$  and  $s_s$ , using annual data for population size, fledging success and numbers of introduced birds, and estimates for all other parameters, and then averaging the results across years.

#### LITERATURE CITED

Wootton, J. T., and D. A. Bell. 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. *Ecological Applications* 2:307–321.

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APPENDIX B. Graphs comparing observed population trajectory of Peregrine Falcons in California and population trajectories predicted if population supplementation of captive breeders had not been terminated.

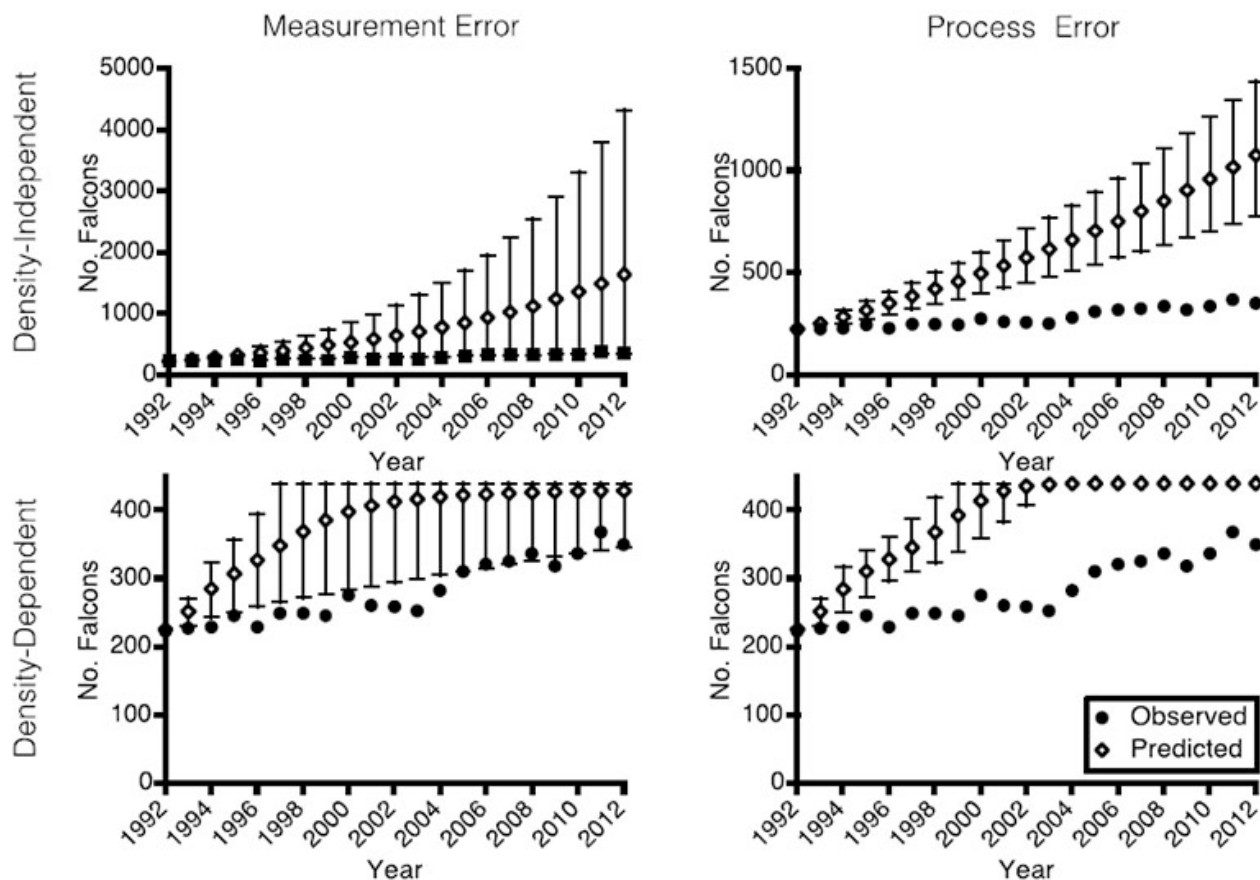


FIG. B1. Comparison of California peregrine falcon population size (mean  $\pm$  95% CI) assuming breeding program had continued at average rates of supplementation, based on 100,000 simulations of the model of Wootton and Bell (1992), compared to observed population size estimated from the number of birds per party hour in CBC counts. Top row: density-independent models, Bottom row: density dependent models, Left column: simulations assuming measurement error, Right column: simulations assuming process error (environmental stochasticity). Observations fall outside of all of the 95% prediction intervals.

LITERATURE CITED

Wootton, J. T., and D. A. Bell. 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. *Ecological Applications* 2:307–321.