

# Demography of a widespread raptor across disparate regions

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Demographic differences between stable and declining populations can lend insight into drivers of population decline. The American Kestrel *Falco sparverius* is a widespread and often-studied falcon, yet its demography is poorly understood, and the causes of observed population declines across much of North America remain unknown. Using integrated population models and sensitivity analysis, we examine how vital rates drive growth in population levels of American Kestrels at four discrete study sites – Florida, Idaho and Pennsylvania with stable nestbox occupancy, and New Jersey, where occupancy is declining. Population growth was most sensitive to changes in adult survival, yet was most correlated with immigration, in all populations. Additionally, population growth was positively correlated with survival rates of juveniles in Pennsylvania. We found evidence for density-dependence in at least one vital rate for all populations except Florida. Fecundity was density-dependent in New Jersey and Idaho, and the population growth rate was density-dependent in Idaho. Adult survival, immigration and the population growth rate were density-dependent in Pennsylvania. The New Jersey population had the highest rate of fecundity, suggesting that declines there are probably not caused by reproductive failure. Our study demonstrates that two principal demographic processes, adult survival and immigration, drive population dynamics of American Kestrels – both of which are understudied.

**Keywords:** demography, *Falco sparverius*, integrated population models, population declines, sensitivity analysis.

Identifying factors that contribute to population regulation is a central element of ecology and conservation biology (Caughley 1994). One powerful method of determining the underlying cause, or causes, of a population decline is to compare the trajectories of populations experiencing different

environmental conditions (Green & Hirons 1991, Green 1995, 2002). Comparing vital rates (e.g. births, deaths, immigration, emigration) of populations on different trajectories can help to identify mechanisms that underlie population declines, thus directing future research and management efforts.

Matrix population models may be used to identify vital rates that most affect the growth of a

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population (e.g. Beissinger & Westphal 1998, Morris & Doak 2002, Norris 2004). The influence of reproduction on population dynamics diminishes along a continuum from 'highly reproductive' species to 'survivor' species (Sæther & Bakke 2000). Raptors are typically long-lived species and are therefore generally considered 'survivor' species (e.g. Ferrer & Hiraldo 1991, Wootton & Bell 1992, Hiraldo *et al.* 1996) – meaning that changes in survival rates tend to affect population growth more strongly compared with changes in reproduction (but see Sergio *et al.* 2011). However, vital rates to which population growth is most sensitive might not be strong drivers of population dynamics because the vital rate with the most sensitivity often varies the least (Gaillard & Yoccoz 2003, Coulson *et al.* 2005). Further inference into mechanistic drivers of population dynamics can therefore be gained by assessing how variation in population growth is driven by variation in vital rates (Schaub *et al.* 2013, Eacker *et al.* 2017, Arnold *et al.* 2018). For example, Robinson *et al.* (2004) showed that changes in juvenile survival probably led to decreases in Song Thrush *Turdus philomelos* populations.

Bird populations are often regulated by density-dependence, whereby vital rates decrease with increased population size (e.g. Lack 1954, Newton 1998, Sæther *et al.* 2016). As populations rise and high-quality nesting sites become saturated, mean fecundity can decline as pairs occupy poorer sites (Rodenhouse *et al.* 1997, Hunt & Law 2000) or as territories become smaller (Sillett *et al.* 2004). Survival can also decrease as resources are depleted and parasite or disease prevalence increases (Newton 1998). Immigration might decrease as territories become saturated (Wilson & Arcese 2008) or increase due to conspecific attraction (Stamps 1988, Schaub *et al.* 2013). Knowledge of density-dependent processes is therefore imperative for understanding population dynamics (Sinclair & Pech 1996).

More than half of all raptor species have declining global populations (McClure *et al.* 2018). In addition, 38% of raptors listed as Least Concern by the International Union for the Conservation of Nature (IUCN 2017) are in decline (McClure *et al.* 2018). The American Kestrel *Falco sparverius* is one of the most widespread raptors in the Western hemisphere. Populations of American Kestrels have been declining across much of North America since at least the 1960s, but the exact causes

still remain to be identified (Smallwood *et al.* 2009a, McClure *et al.* 2017b). The American Kestrel is listed as endangered or threatened in New Jersey (New Jersey Department of Environmental Protection 2017), Florida (Florida Fish & Wildlife Conservation Commission 2012), Connecticut (Connecticut Department of Energy & Environmental Protection 2015) and Delaware (Delaware Department of Natural Resources & Environmental Control 2015), and is mentioned as a species of concern in 21 US State Wildlife Action Plans ([www1.usgs.gov/csas/swap/](http://www1.usgs.gov/csas/swap/)). American Kestrels are generally well studied (Buechley *et al.* 2019) but population dynamics are surprisingly poorly understood and are a research priority (McClure *et al.* 2017b). To our knowledge, few studies have calculated apparent survival for American Kestrels (e.g. Bortolotti *et al.* 2002, Hinnebusch *et al.* 2010, Brown & Collopy 2013), one study has estimated immigration (Brown & Collopy 2013), and no study has conducted a sensitivity analysis or examined density-dependence.

Here, we examine four different aspects of population regulation of American Kestrels at four discrete study sites – Florida, Idaho and Pennsylvania with stable breeding populations, and New Jersey, where the breeding population is declining. We use integrated population models (IPMs; Besbeas *et al.* 2002, Abadi *et al.* 2010b, Schaub & Abadi 2011) to estimate and compare vital rates among sites, calculate elasticities and determine which vital rates correlate most closely with population growth. We also examine density-dependence and determine which vital rates change as populations increase or decrease. We predicted that population growth would be most sensitive to adult survival (e.g. Ferrer & Hiraldo 1991, Wootton & Bell 1992, Hiraldo *et al.* 1996), although immigration would correlate more with yearly growth (Brown & Collopy 2013, Schaub *et al.* 2013). We further predicted that levels of survival or immigration would be lower in the declining population, whereas levels of fecundity would be relatively equal across sites.

## METHODS

### Study organism, site and field methods

We studied the demography of American Kestrels associated with networks of nestboxes at four study sites in the USA, North America:

northwestern New Jersey, southwestern Idaho, southeastern Pennsylvania and north-central Florida (Fig. 1, Table S1). Establishment, monitoring and maintenance protocols varied but, in general, wooden nestboxes were placed in open to semi-open vegetation on trees, utility poles, wooden posts or road sign supports. We visited nestboxes during late winter or early spring to clean and make repairs. Boxes were then checked for American Kestrel eggs or young throughout spring and early summer, with recheck intervals varying from 3 to 24 days (Table S1). We also attempted to identify any marked American Kestrels encountered. Nearly all nestlings were banded, and in New Jersey and Florida, most were fitted with unique patagial tags, at 21–24 days old. We considered nestlings to have successfully fledged if they reached 80% of fledging age (approximately 22 days; Steenhof & Newton 2007).

We also captured and marked adult American Kestrels. In Florida and New Jersey, we attempted to trap all adult females inside boxes with a custom-made net on an extendable painter's pole. In New Jersey, we trapped adults throughout the typical 30-day incubation period, whereas in Florida, they were trapped near the end of incubation. We confirmed the identity of recaptured adults, and banded and individually marked all newly captured adults with either patagial tags with unique alphanumeric characters or unique combinations of coloured patagial tags (Smallwood & Natale 1998). In Idaho and Pennsylvania, we usually trapped adults by blocking the nestbox entrance and manually removing incubating or brooding American Kestrels. On some occasions we trapped adults by using a mist-net with a live Great Horned Owl *Bubo virginianus* (Steenhof *et al.*

1994) or using a *bal-chatri* with a mouse as bait. We followed established guidelines for the use of wild birds in research (Fair *et al.* 2010) and conducted research under Boise State University IACUC Numbers 006-01-006 and 006-05-004, University of Nevada Reno IACUC 00329, and Montclair State University IACUC 2016-027. We did not analyse and do not present data from the first 5 years of each monitoring programme to avoid including data during an occupancy lag, when trends in nestbox occupancy do not reflect trends in population levels (McClure *et al.* 2017a).

### Modelling framework

We estimated survival probabilities, fledgling production, population growth rates and immigration rates with integrated population models in R 3.3.1 (R Core Team 2015). Each population was modelled separately, but the integrated population models were generally structured similarly. We used three components to inform the age-structured state-space models in our female-based IPMs: a population census or index, fecundity estimates, and a mark–recapture model of our marked adults and nestlings (further details of the model structures and likelihoods are given in Appendix S1, and sample R code in Appendix S2; Abadi *et al.* 2010a, Schaub & Abadi 2011). Our mark–recapture datasets were derived from the resightings and recaptures of American Kestrels initially marked as either adults or nestlings. We modelled fecundity (i.e. the number of female offspring per breeding female per year) by observing nesting attempts in the monitored nestboxes. In Florida, our index to population size was simply the numbers of confirmed breeding females occupying nestboxes, because the same nestboxes were observed for the duration of this study. This provided a conservative estimate of the actual size of the breeding population, because pairs sometimes chose natural cavities within their territories rather than nestboxes. At the other three study sites, the number and identity of nestboxes varied during the study. Therefore, we estimated the population size from the number of nestboxes used for breeding (e.g. the number of observed breeding females) divided by the total number of nestboxes monitored that year. In Idaho, nestbox monitoring data were missing for the year 2007, so we needed to impute the missing population size index value. Thus, we initially modelled the Idaho population



**Figure 1.** Map of the study sites (points) in each of the four states.

size index as a Poisson model of the number of occupied boxes, supplying the number of boxes monitored as an offset. We then used the rounded mean of the estimated number of occupied nestboxes as the population size index for that year. Similarly, we were missing data for Florida for 2011. Because we had data describing the observations from every nestbox check in Florida, we initially modelled the nestbox population with a dynamic occupancy model (Kéry and Schaub, 2012). Again, the missing data in Florida for the population size for the IPM was imputed from the output of this initial model. We considered annual datasets as independent, even though many of the same adult females were represented in multiple years. A simulation study by Abadi *et al.* (2010a) examined the impacts of violation of the assumption of independence and found minor impacts on the accuracy of parameter estimates for moderate-sized datasets.

### State-space model

We modelled our American Kestrel populations with state-space models that combined a process model (latent or unobserved) describing the underlying process that generated the collected data with an observed model that describes the data, as observed, given the process model (De Valpine & Hastings 2002; Appendices S1 and S2). Our general process model was based on a simple two-age projection matrix model considering yearlings ( $N_1$ ) and adults age 2 and older ( $N_{ad}$ ), because American Kestrels are capable of breeding as yearlings, they probably breed every year once recruited, and fecundity does not generally appear to depend on age (Caswell 2001, Smallwood & Bird 2020, but see Steenhof & Heath 2009). The expected number of female American Kestrels at time  $t + 1$  was the number of female immigrants in year  $t + 1$  ( $N_{imm}$ ) plus the product of the population vector in year  $t$  and the projection matrix, with  $\phi_{juv,t}$  and  $\phi_{ad,t}$  the juvenile and adult apparent survival probabilities, and  $f_t$  the fecundity or the expected number of female offspring per breeding female at year  $t$  ( $N_{1,t+1}$  and  $N_{ad,t+1}$ ; Abadi *et al.* 2010b, Schaub & Fletcher 2015).

Following other authors (e.g. Kéry & Schaub 2012), we introduced additional demographic stochasticity to the population process model by modelling the number of females in each age class with Poisson, binomial and uniform distributions:

$$N_{1,t+1} \sim Po\left((N_{1,t} + N_{ad,t} + N_{imm,t})f_t\phi_{juv,t}\right) \quad (1)$$

$$N_{ad,t+1} \sim Bin\left((N_{1,t} + N_{ad,t}),\phi_{ad,t}\right) \quad (2)$$

$$N_{imm,t+1} \sim Unif(0, 100) \quad (3)$$

The three different parameterizations of the groups in the state-space model reflect biology and our best approximation of the expected processes that led to the observed numbers. Beginning with the adult birds, we considered the number of those to be a function of the survival rate and the size of the population in the previous year, which is most naturally modelled as a binomial function. Meanwhile, the young birds were modelled as a birth process from the number of breeding individuals, which typically is thought of as a distribution of integers (whole numbers) generally following the Poisson distribution. In the absence of additional information, we considered the number of immigrants to be essentially a purely random number. In this case, to impose the least amount of structure possible on our estimate, we considered the possible number of immigrants to be anything from zero to a reasonably large number of new individuals with no particular value more likely than any other – hence, the use of a uniform distribution.

We considered the observation process as a Poisson process conditional on the state process:

$$y_t \sim Po(N_{1,t} + N_{ad,t} + N_{imm,t}) \quad (4)$$

where  $y_t$  was the number of observed breeding females in year  $t$ . The overall average population growth rate was estimated as the geometric mean of the annual probabilities (Williams *et al.* 2002). See Appendix S1 for more details, and Appendix S2 for example R code.

### Capture-mark-recapture model

We modelled apparent annual survival probabilities, which confound emigration and true survival, of adult female American Kestrels ( $\phi_{ad}$ ) and post-fledging juvenile American Kestrels ( $\phi_{juv}$ , both sexes pooled) using a Cormack–Jolly–Seber model (Cormack 1964, Jolly 1965, Seber 1965, Lebreton *et al.* 1992). Survival probabilities were modelled with random effects of time. Recapture

probabilities ( $p_{ad}$  and  $p_{juv}$ ) differed by age-class but were modelled as constant over time because recapture and resighting efforts were generally equal across years within studies.

### Fecundity

Fecundity,  $f$ , was estimated from half of the observed fledglings (assumed sex ratio of 50 : 50),  $J$ , and the number of reproducing females,  $R$ . Thus,  $J_t$  was assumed to follow a Poisson distribution with a random temporal component:

$$J_t \sim Po(R_t f_t) \quad (5)$$

### Model run details

All prior probabilities were selected to be uninformative or weakly informative (Appendices S1 and S2). For each model, we ran three chains for 40 000 iterations, discarding the first 10 000 runs as burn-in, and then drawing 2000 samples for parameter estimates. We assessed convergence by visual inspection of the model trace, and the Raftery–Lewis and Gelman–Rubin diagnostic tests implemented in the R package ‘coda’ (Gelman & Rubin 1992, Plummer *et al.* 2006). We assessed model fit by posterior predictive checks or Bayesian  $P$ -values (Hobbs & Hooten 2015). Briefly, we simulated a new dataset at each iteration of the converged chains. We then computed the proportion of times that the estimate of mean, coefficient of variation or sum of squares of model fit of the simulated data set exceeded the corresponding estimate from the observed dataset. If this statistic was close to 0 or 1, we concluded that the model did not represent the distribution of the data well.

### Elasticity analysis

We calculated the elasticity of  $\lambda$  to changes in vital rates for each site by building a deterministic population matrix (Caswell 2001) for each sample of posterior distributions. Each matrix was built as:

$$\begin{bmatrix} f * \phi_{juv} & f * \phi_{juv} \\ \phi_{ad} + imm & \phi_{ad} + imm \end{bmatrix} \quad (6)$$

. We then used the `vitalsens()` function in the `popbio` package (Stubben & Milligan 2007) in R to estimate elasticities for each parameter in each

matrix. By using the entire posterior distributions instead of point estimates of vital rates, we were able to estimate the uncertainty associated with elasticities.

### Annual variation in vital rates and density-dependence

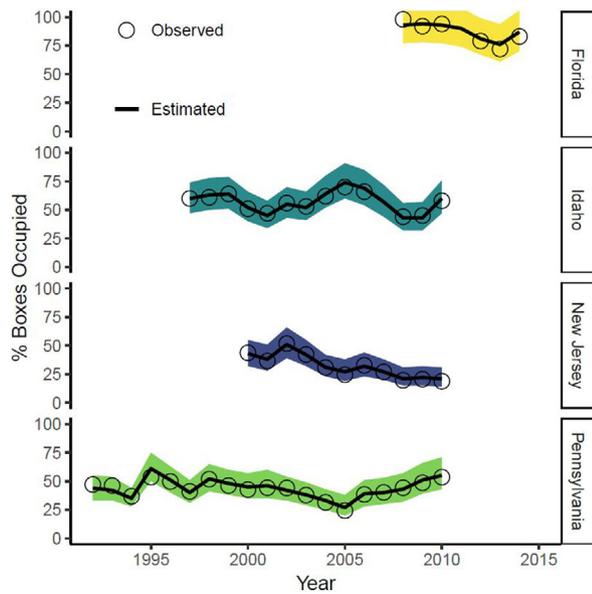
To determine which vital rates correlated most with yearly changes in  $\lambda$ , we created linear models with draws from the posterior distributions of yearly vital rates and  $\lambda$  for each study site to determine which vital rates correlated most with yearly changes in  $\lambda$  (Kéry & Schaub 2012, Schaub *et al.* 2013). We created linear models with the yearly posterior draws of vital rates or  $\lambda$  and the posterior draws of the population size index to assess density-dependence (Schaub *et al.* 2013). We highlight parameter estimates for which the 95% or 90% credible intervals of correlation coefficients ( $r$ ) excluded zero.

## RESULTS

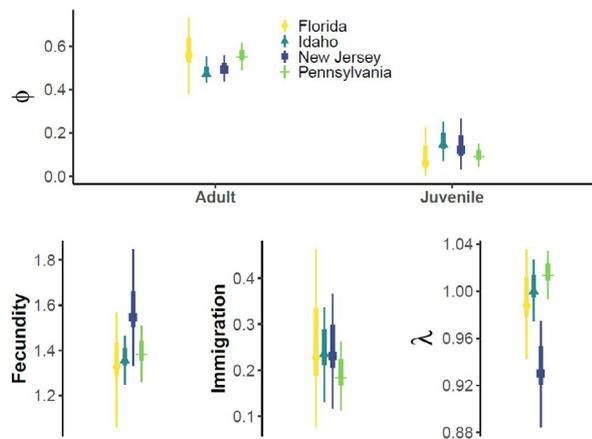
Monitoring durations varied from 7 to 19 years at the four study sites, and the number of nestboxes monitored ranged from 61 to 217 per year (Table S1). Observed occupancy rates for nestboxes were as low as 19% in New Jersey and as high as 86% in Florida. We uniquely marked a total of 4252 fledgling female American Kestrels and 1050 adult female American Kestrels.

All models fit the data well with Bayesian  $P$ -values near 0.50, Gelman–Rubin statistics  $< 1.1$ , and trace plots indicating good mixing of chains. Furthermore, the observed population indices matched the estimated values at each site well (Fig. 2). As expected, the population in New Jersey had the lowest population growth rate, followed by Florida, Idaho and Pennsylvania (Fig. 3, Table 1). Levels of survival and immigration were not lower in New Jersey than at the other sites, but fecundity was higher in New Jersey (Fig. 3, Table 1).

Elasticity values were similar across all sites, with  $\lambda$  being far more sensitive to changes in adult survival than to other vital rates (Fig. 4, Table 1). Yearly variation in population growth rates correlated with immigration at all sites and with juvenile survival in Pennsylvania (Fig. 5). Density-dependence was apparent in adult survival, immigration and  $\lambda$  in Pennsylvania, fecundity in New Jersey and  $\lambda$  in Idaho, but no vital rates in Florida (Fig. 6).



**Figure 2.** Percent of nestboxes occupied by American Kestrels at study sites in New Jersey, Idaho, Pennsylvania and Florida, USA. Black lines represent yearly estimates from integrated population models. Shaded areas are the 95% credible intervals of estimates and open circles represent observed values.



**Figure 3.** Caterpillar plots indicating estimates of adult and juvenile apparent survival ( $\phi$ ), fecundity, immigration and population growth rate ( $\lambda$ ). All parameters were estimated using integrated population models. Points represent medians of posterior probability distributions, thick lines represent 68% credible intervals and thin lines represent 95% credible intervals.

## DISCUSSION

We found that the principal driver of population growth ( $\lambda$ ), immigration, was similar across a continent within the same species of conservation

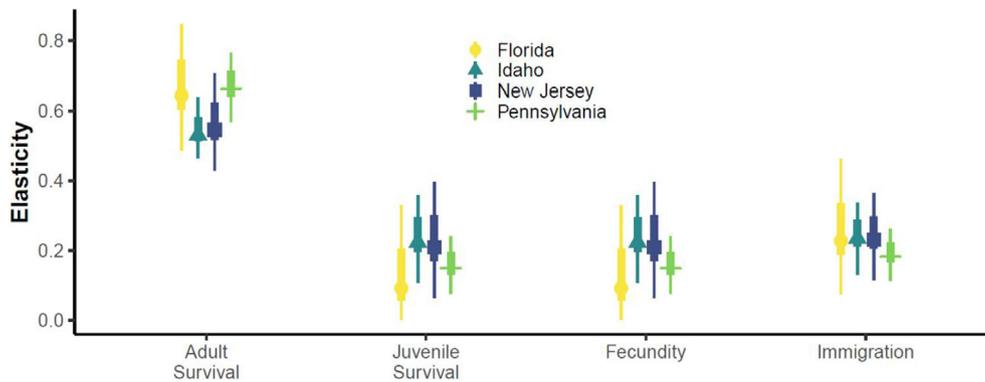
concern. Perhaps the most salient of our findings is that the declining population in New Jersey had the highest rate of fecundity. It is therefore unlikely that declines in New Jersey are the result of low reproductive rates or lack of suitable nest-sites (McClure *et al.* 2017a) but rather are caused by low fledgling survival, mortality outside of the breeding season (Smallwood *et al.* 2009a), or an imbalance between emigration and immigration. Indeed, relatively high elasticity of apparent adult survival across all sites indicates that management of adult survival would affect population growth for American Kestrels more than management of other vital rates would (e.g. Beissinger & Westphal 1998, Morris & Doak 2002, Norris 2004). Our results therefore support past calls for research on the migratory connectivity and survival of American Kestrels during the non-breeding season (McClure *et al.* 2017b). We also recognize that fecundity, as measured by the number of young reaching 80% of fledging age, is an imperfect estimate of productivity (Streby *et al.* 2014). A more informative measure might incorporate post-fledging survival of young American Kestrels to nutritional independence, but we were unable to do so at any of our study sites.

Management of the most elastic vital rates will affect population growth most, but the most elastic vital rates often vary the least between years (Gaillard & Yoccoz 2003, Coulson *et al.* 2005). Yearly changes in population levels are commonly driven by less elastic vital rates. Our results generally support this assertion, with yearly population growth of all study populations being uncorrelated with the most elastic vital rate, adult survival. Indeed, contrary to our prediction, adult survival was not the primary driver of annual population fluctuations for this raptor species. Similarly, a study of Black Kites *Milvus migrans* indicated that survival of juveniles before they reach reproductive maturity was the primary driver of population growth rate (Sergio *et al.* 2011). Here, immigration was correlated with yearly population growth at each North American study site and thus disproportionately drove annual changes in population levels.

We estimated immigration as a latent parameter in our model. Therefore, once the occupancy and demographic data were integrated, the immigration parameter was estimated based on left-over, unexplained variation. This unexplained variation represents immigration because the model has

**Table 1.** Mean (sd) and elasticities (sd) of population growth rates ( $\lambda$ ), adult ( $\phi_{\text{adult}}$ ) and juvenile ( $\phi_{\text{juvenile}}$ ) survival rates, fecundities, and immigration rates for American Kestrels at four study sites. The  $\lambda$  estimates are derived from integrated population models, not Lefkovich matrices

	Parameter	New Jersey	Idaho	Pennsylvania	Florida
Rates	$\lambda$	0.93 (0.02)	1.00 (0.01)	1.01 (0.01)	0.99 (0.02)
	$\phi_{\text{juvenile}}$	0.13 (0.06)	0.15 (0.05)	0.09 (0.03)	0.08 (0.06)
	$\phi_{\text{adult}}$	0.50 (0.03)	0.48 (0.03)	0.55 (0.03)	0.56 (0.08)
	$\rho_{\text{juvenile}}$	0.35 (0.15)	0.55 (0.14)	0.25 (0.06)	0.50 (0.19)
	$\rho_{\text{adult}}$	0.29 (0.07)	0.69 (0.07)	0.29 (0.04)	0.91 (0.08)
	Immigration	0.21 (0.06)	0.21 (0.05)	0.15 (0.04)	0.20 (0.09)
	Fecundity	1.55 (0.13)	1.36 (0.05)	1.38 (0.06)	1.32 (0.13)
Elasticity	$\phi_{\text{juvenile}}$	0.21 (0.09)	0.23 (0.07)	0.15 (0.04)	0.11 (0.09)
	$\phi_{\text{adult}}$	0.55 (0.07)	0.54 (0.05)	0.66 (0.05)	0.65 (0.09)
	Immigration	0.23 (0.07)	0.24 (0.05)	0.18 (0.04)	0.24 (0.01)
	Fecundity	0.21 (0.09)	0.23 (0.07)	0.15 (0.04)	0.11 (0.09)

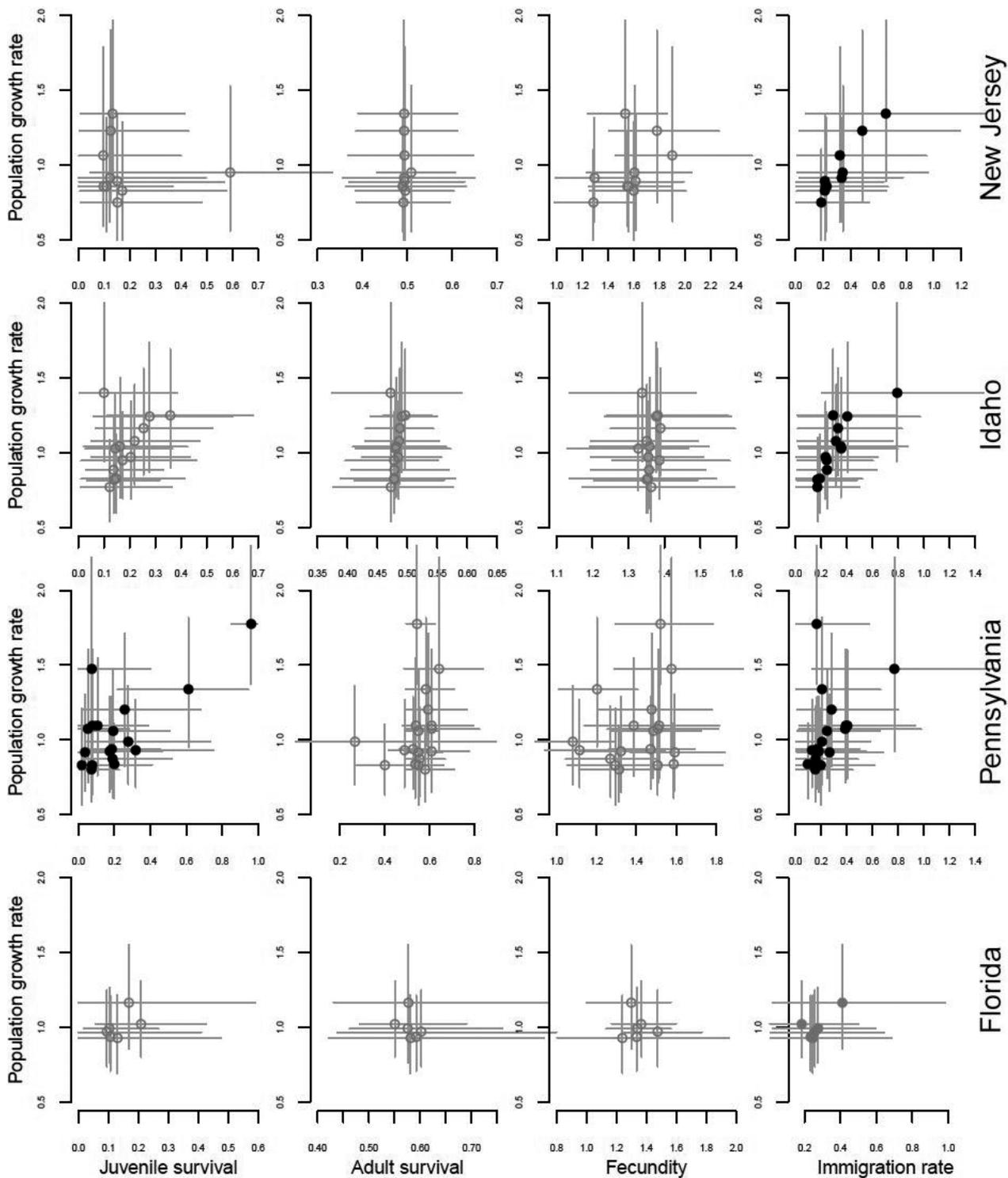


**Figure 4.** Elasticities of adult and juvenile survival, fecundity and immigration at four sites across the USA. Estimates were calculated by randomly sampling the posterior distributions of vital rates presented in Figure 2. Points represent medians of posterior probability distributions, thick lines represent 68% credible intervals and thin lines represent 95% credible intervals.

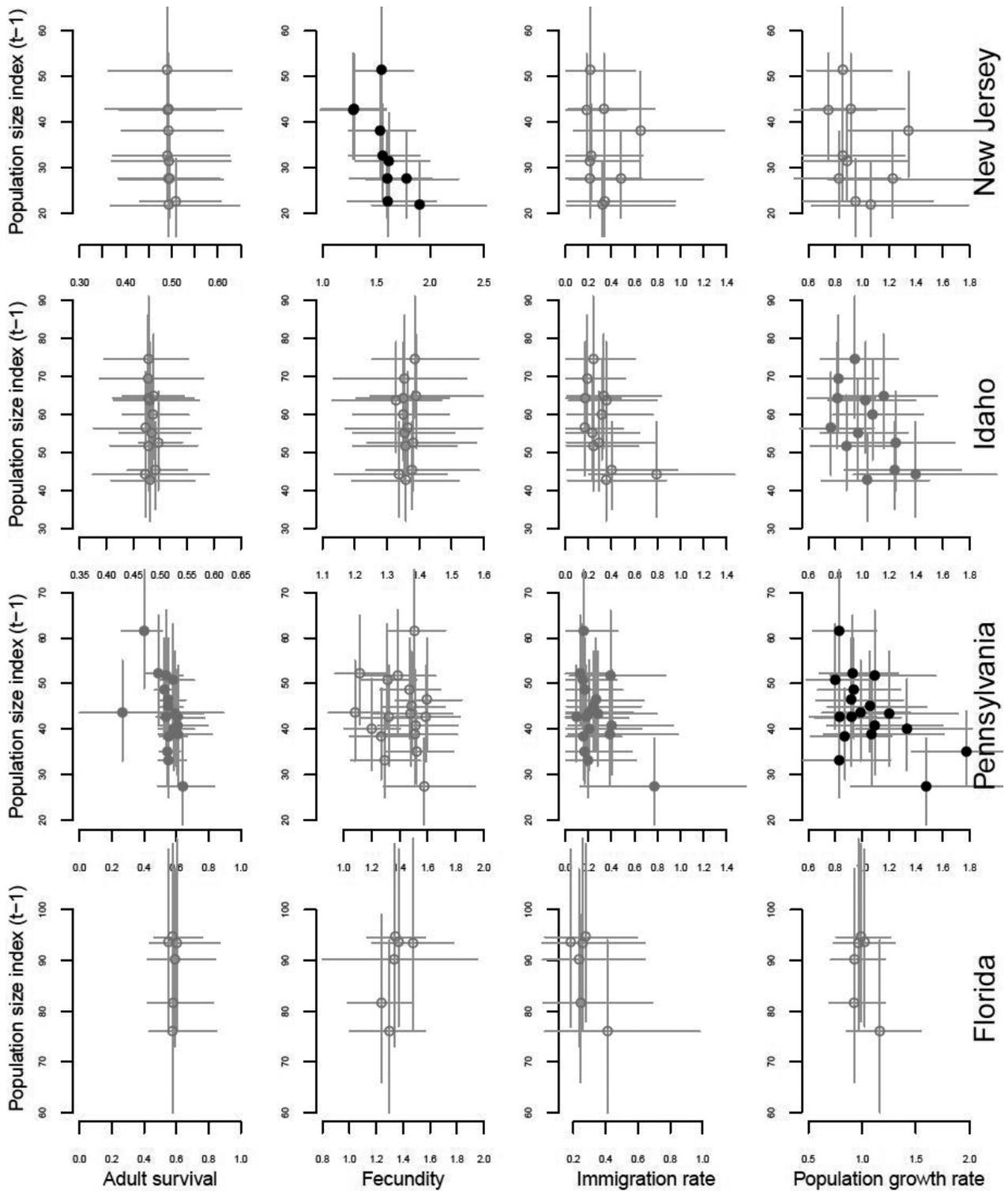
empirical data on other the population parameters (fecundity and apparent survival). Our immigration and survival estimates therefore lend limited insight into dispersal patterns. We estimated apparent survival, which is a combination of both true survival and emigration. Therefore, our immigration and survival estimates are affected by dispersal both to and from other areas, and between natural cavities and nestboxes. Natal dispersal was likely to be partially responsible for the low rates of apparent juvenile survival across all study sites. Steenhof and Heath (2013) found that only 4% of locally produced American Kestrels returned to reproduce in our Idaho study site. Furthermore, McCaslin *et al.* (2020) found that long-distance dispersal (> 30 km) is relatively common in

American Kestrels. Brown and Collopy (2013) demonstrated that immigration was integral to population stabilization in Florida. Our results further suggest that dispersal is, in general, a key component of American Kestrel population dynamics and should be a research and management priority.

No two populations in our study showed density-dependence in the same sets of vital rates, even for the two relatively nearby populations (New Jersey and Pennsylvania). Variation in density-dependence across these populations probably represents differing abundances of prey, nest-sites, parasites and predators, among many other factors (e.g. Rodenhouse *et al.* 1997, Newton 1998, Hunt & Law 2000, Sillett *et al.* 2004). Apparently, these



**Figure 5.** Plots of yearly vital rates vs. the population growth rate. Open circles indicate mean estimates, and lines represent the 95% credible intervals. Black closed circles indicate that the probability of the correlation coefficient ( $r$ )  $> 0$  is  $\geq 0.95$ . Grey closed circles indicate that the probability of  $r > 0$  is  $\geq 0.90$  but  $< 0.95$



**Figure 6.** Plots of vital rates vs. the population size index. Open circles indicate mean estimates, and lines represent the 95% credible intervals. Black closed circles indicate that the probability of the correlation coefficient ( $r > 0$ ) is  $\geq 0.95$ . Grey closed circles indicate that the probability of  $r > 0$  is  $\geq 0.90$  but  $< 0.95$ .

populations experienced differing pressures that manifested in different rates of density-dependence, even given similar vital rates. A similar phenomenon was documented in three gamebird species that showed variation in density-dependence at 10 sites across the state of Kansas, USA (Williams *et al.* 2003).

Lambrechts *et al.* (2010) cautioned that differences in nestbox management could complicate comparisons of demography among study sites. Our methods were generally similar across our study areas, but some differences were unavoidable. For example, several nestboxes in Idaho had to be removed over the course of the study because of road construction and urban sprawl. The areas from which these boxes were removed tended to be of low fecundity compared with the rest of the study site (Strasser & Heath 2013). Similarly, seldom-occupied or unproductive boxes were either removed or left unmonitored after several years in Florida and Pennsylvania (Katzner *et al.* 2005). Occupancy rates in nestboxes are also affected by trends in availability of unmonitored cavities (McClure *et al.* 2017a). Unobserved trends in deforestation, succession, and unaffiliated nestboxes within and surrounding our study sites could thus have affected our results. Such stochastic and unknown effects are unavoidable in areas not under strict control of researchers. Simulations should be conducted to estimate the consequences of these effects, especially in the context of integrated population models. Finally, we are unaware of studies examining the effects of patagial tags on survival of American Kestrels. However, these tags do not affect breeding success (Smallwood & Natale 1998, Smallwood 2016). We recommend future studies to determine whether patagial tags are detrimental to American Kestrels.

The demography of other kestrel species provides context for our results. For example, density-dependent processes are important for the dynamics of Mauritius *Falco punctatus* (Nicoll *et al.* 2003) and Lesser Kestrels *Falco naumanni* (Di Maggio *et al.* 2016). Moreover, Hiraldo *et al.* (1996) showed that population growth of Lesser Kestrels in southern Spain was most sensitive to changes in adult survival, whereas fecundity is a prominent driver of population change in a population of Eurasian Kestrels *Falco tinnunculus* in Switzerland (Fay *et al.* 2019). Given the similar life-histories of kestrel species, inference from the population

dynamics of other kestrels might inform the conservation of the American Kestrel.

Demography can vary across the range of a given species (e.g. Brown 1995, Angert 2009, Purves 2009) and thus large-scale demographic monitoring programmes (e.g. Iliff *et al.* 2008, Ahrestani *et al.* 2017, Arnold *et al.* 2018) with standardized methodology (Anderson *et al.* 2017) are needed to examine range-wide phenomena. As technology increases the ability of scientists to collaborate and share data, researchers should develop partnerships to combine their individual efforts into continental, or even global, monitoring programmes.

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### Data Availability Statement

The data that support the findings of this study can be obtained upon reasonable request from the corresponding author.

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## SUPPORTING INFORMATION

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

**Appendix S1.** Joint likelihood and prior probabilities of the integrated population models.

**Appendix S2.** Example of R code used in analysis.

**Table S1.** Studies that provided demographic data for American Kestrels (*Falco sparverius*).