REPRODUCTION VERSUS RECRUITMENT OF SWAINSON'S HAWKS IN THE BUTTE VALLEY, CALIFORNIA

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Abstract. Measures of reproductive success have long been assumed to be reasonable surrogates of fitness. We examined reproductive success and recruitment at the individual and population levels in Swainson's Hawks breeding in northern California. At the population level, we investigated whether the number of individuals subsequently recruited could be predicted by the number of offspring produced in any given year, finding no evidence of differences in probability of recruitment by cohort or year. Instead, age of recruits was the best predictor of probability of their being recruited into the local breeding population. At the individual level, we used generalized linear models to examine the correlation between lifetime reproductive success of individual females and the number of their offspring recruited. For individuals, the number of fledglings produced was significantly correlated with both the number of those offspring and of grandchildren recruited into the breeding population. We also examined the relationship between the average annual reproduction of an individual and the number of offspring recruited, finding these significantly correlated. The relationship was not linear: individuals producing moderate numbers of fledglings, on average, yielded the highest numbers of recruits, reflecting a trade-off between adult survival and reproduction. These results provide evidence that monitoring of reproductive success of individuals or a population can give reasonable indices of future recruitment if the study is continued for a long period. But individuals with the highest average rate of reproduction may not be the most fit.

Key words: Buteo swainsoni, *fitness, lifetime reproductive success, recruitment, reproduction, Swainson's Hawk.*

Reproducción Versus Reclutamiento de *Buteo swainsoni* en el Valle de Butte, California

Resumen. Las mediciones de éxito reproductivo han sido asumidas desde hace mucho tiempo como sustitutos razonables de la adecuación biológica. Examinamos el éxito reproductivo y el reclutamiento a niveles individual y poblacional en individuos de *B. swainsoni* reproduciéndose en el norte de California. A nivel poblacional, investigamos si el número de individuos reclutados subsecuentemente podía ser predicho por el número de descendientes producidos en cualquier año, no encontrando evidencia en las diferencias de la probabilidad de reclutamiento por cohorte o año. En cambio, la edad de los individuos reclutados fue lo que mejor predijo la probabilidad de ser reclutados en la población reproductiva local. A nivel individual, usamos modelos lineales generalizados para examinar la correlación entre el éxito reproductivo a lo largo de la vida de hembras individuales y el número de su descendencia reclutada. Para los individuos, el número de volantones producidos se vio significativamente correlacionado con el número de esos descendientes y con el de los nietos reclutados en la población reproductiva. También examinamos la relación entre la reproducción media anual de un individuo y el número de descendientes reclutados, encontrándolos significativamente correlacionados. La relación no fue lineal: los individuos que producen un número moderado de volantones, en promedio, produjeron los números más elevados de reclutas, reflejando una solución de costo-beneficio entre la supervivencia del adulto y su reproducción. Estos resultados proveen evidencia de que el monitoreo del éxito reproductivo de individuos o de una población puede brindar índices razonables de reclutamiento futuro si el estudio se continúa por un período de tiempo largo. Sin embargo, los individuos con la tasa más elevada de reproducción pueden no ser los más aptos.

INTRODUCTION

Reproductive success has long been used as a surrogate of other factors of interest, such as habitat quality (e.g., Newton 1989) or individual quality (e.g., Packer et al. 1988). The implicit assumption of most of these studies and justification for this measure is that annual reproductive success of a population or lifetime reproductive success of an individual is a good proxy for the proportion of genetic contribution to future generations (i.e., fitness). This assumption, however, may be poor (Grafen 1988, Murray 1992) and has rarely been examined at the population or individual level because of the difficulty in assessing

other measures of fitness, as in some species it takes years for young to be recruited into the breeding population. The situation is often further complicated by emigration of young and subadults from the local population. Survival of young varying with natal conditions (e.g., Naef-Daenzer et al. 2001, Moreno et al. 2005) may cause reproductive success to be a poor indicator of fitness. Therefore, it is important to test this underlying assumption widespread in the ornithological literature.

Despite the difficulties in measuring true fitness (i.e., the contribution of genes to future generations), one can measure recruitment through standard mark–recapture techniques, which is likely to be a better proxy for fitness than reproductive success alone (McGraw and Caswell 1996). By examining recruitment of cohorts (i.e., all individuals produced within the same year), we can begin to determine if there are factors that affect survival or recruitment of cohorts differentially. Recruitment of young from individuals is also likely to be a better indication of fitness than lifetime reproductive success alone. Most studies that have examined the relationships between lifetime reproductive success and recruitment in migratory populations have demonstrated a positive correlation between lifetime reproductive success and offspring recruitment (e.g., Hotker 1988, Postupalsky 1989, Weatherhead and Dufour 2000, Wiens and Reynolds 2005). Along the same line, measuring grandchildren is likely an even better surrogate of fitness than either lifetime reproductive success or recruitment of offspring, as it may also account for quality of the offspring.

Because of logistic constraints, however, few studies have monitored marked individuals over the course of a lifetime; therefore, it is necessary to also examine the relationship between annual reproductive success of the population and subsequent recruitment of that cohort. In studies that have reported such population-level recruitment, results are equivocal. For example, Wiens and Reynolds (2005) reported that there was no correlation between the number of chicks fledged in a breeding season and the number of chicks from that cohort subsequently recruited in a population of the Northern Goshawk (*Accipiter gentilis*). In contrast, in a population of the Red-winged Blackbird (*Agelaius phoeniceus*) Weatherhead and Dufour (2000) reported a significant positive correlation between the two measures, highlighting the potential variability in these measures and the need for further study of the utility of reproductive success as an accurate predictor of recruitment, and by extension, fitness.

One factor that may help explain differences in results are density-dependent effects. Populations at carrying capacity might show a decreased relationship between population-level reproduction and recruitment of those offspring because of limited habitat availability (Hochachka et al. 1989, Arcese et al. 1992). Therefore, it may be necessary to account for potential competition between members of cohorts to determine if density dependence is influencing the number of offspring that are able to be recruited into a local breeding population.

To test these assumptions, we analyzed a long-term dataset for a population of Swainson's Hawk (*Buteo swainsoni*) that nests in the Butte Valley, California. We assessed whether lifetime reproductive success was a reasonable predictor of recruitment (i.e., individual-level recruitment) and whether the number of individuals produced in a cohort was similarly correlated to the number of individuals recruited into the breeding population (i.e., population-level recruitment). For this analysis, we first expect there to be differences in the age at first recruitment into the population. If there are differences in the probability of individuals being recruited into the breeding population, we would expect that year of fledging should explain differences in recruitment between cohorts. Thus, if there are no differences by cohort in probability of recruitment, we expect models incorporating age at first recruitment, alone, to describe our data best. We also assessed whether the number of grandchildren (i.e., number of offspring's offspring) recruited into the breeding population was correlated with lifetime reproductive success. Finally, to better compare recruitment with other studies we examined the mean seasonal reproductive output of each individual with the number of recruits and grandchildren it produced.

METHODS

In 1979, surveys for Swainson's Hawks began in the Butte Valley of California (41° 49′ N, 122° 0′ W) with the goal of contributing to an overall assessment of the Swainson's Hawk population in California. During these initial surveys, breeding adults were trapped and marked with uniquely numbered plastic color bands to identify each bird individually; nestlings were banded with U.S. Geological Survey (USGS) metal bands. Hawks were trapped with a dho-gaza with a Great Horned Owl as a lure (*Bubo virginianus*: Bloom et al. 1992) or bal-chatri with a mouse or sparrow as a lure. Partial surveys of the valley continued through 1986. In 1987, the surveys were expanded to include the entire valley floor to census the population. The population was monitored intensively through the late 1990s. From 1999 to 2009 survey effort varied because of varying numbers and experience of field technicians; however, we attempted to census the population nesting within the study area completely each year from 1987 to 2007.

Before nesting, adults were observed for signs of mating behavior (e.g. undulating flight, copulation, nest building, etc.). The valley floor was surveyed by vehicle and by foot. High road densities, facilitated by the agricultural nature of the valley, allowed much of the surveying to be done from vehicles, which helped minimize disturbance of breeding pairs. Once pairs were identified they were observed until nest sites were located. Nest trees were not approached until a week after the mean date of hatching (June 16) to avoid nest abandonment (Woodbridge 1991). Nests were generally located in or near the top of western junipers (*Juniperus occidentalis*; Woodbridge 1991) and were accessed by free climbing the tree or with tree spikes and lanyards when necessary. The number and approximate age of nestlings were recorded whenever possible, and nestlings were

banded with USGS aluminum bands when they reached approximately 3 weeks of age. Because of logistic constraints of monitoring nests until fledging, we considered chicks fledged once they reached at least 80% of fledging age (Steenhof 1987). We counted individuals as recruited when they were caught in a subsequent year or their aluminum band was read through a spotting scope and they were confirmed engaging in nesting behavior (e.g., territory defense, nest building, copulation). Therefore an individual did not need to breed successfully to be included as a "recruit."

STATISTICAL ANALYSES

To analyze population-level recruitment we created a multistate model in program MARK (Burnham and White 1999, Reed et al. 2003). The dataset consisted of all individuals banded as nestlings, with those individuals recruited into the population transitioning from a prebreeder state to a breeder state. Here we define a prebreeder as an individual that has fledged but has not yet been observed breeding. We modeled adults' survival rates with linear and quadratic temporal trends, as suggested by previous studies (Briggs 2007). The probability of a breeder transitioning to a prebreeder was fixed at zero (i.e., once an individual became a breeder we considered it always a breeder), as was the rate of recapture of nonbreeders, because nonbreeders are not typically observed in the study area. In addition, survival of prebreeders was fixed at 1. Naturally, we do not expect prebreeders' survival to even approach 1 but assigned this value merely as a statistical construct necessitated by the relative sparseness of the data and our inability to estimate both prebreeders' survival and transition probability separately. Therefore, the transition probability (Ψ) was a combination of both the probability of an individual's survival from fledging to breeding and its recruitment into the local population.

To examine population-level recruitment, we explored three general hypotheses: annual differences, cohort differences, and age differences in transition probability. As age at recruitment could drive model structure, we also examined additive models of age at recruitment, cohort differences, and annual differences. Because our dataset was sparse, it was necessary to limit parameter estimation by grouping time or age in our models. Time and age were grouped into blocks of 2, 3, and 5 years so that blocks of years were given the same parameter estimate. This procedure forces years or ages close together to have the same value. Additionally, we examined each parameter with linear and quadratic trends. If the quality of cohorts differs, then we expect that models specifying transition probability differing by cohort will be strongly supported. If models incorporating annual variation in transition probability are the best, this would also support the hypothesis that there are differences in survival and/or recruitment of cohorts, and that an individual's reproductive success is not necessarily a good measure of fitness because annual effects drive differences in recruitment of offspring. Finally, if the probability of an individual being recruited into the breeding population is not affected by density-dependent factors or annual factors, models incorporating age in transition probability will be strongly supported.

We also used two annual group covariates to investigate density-dependent effects. First, we used the total number of fledglings observed in the study area annually and compared that number to the probability that an individual of that cohort would be recruited into the local breeding population. As not all nests were observed each year and therefore offspring could have been missed, we also used the mean number of fledglings produced per nest as an index of the effect of potential future intraspecific competition on recruitment into the breeding population (i.e. density-dependent recruitment). We used Akaike's information criterion adjusted for small samples sizes (AIC_c, Burnham and Anderson 2002) to compare the models in program MARK. We checked for overdispersion, using program U-CARE to estimate $\hat{c}$ (Choquet et al. 2005). Finally, we used the AIC_c weights (w_i) to account for model uncertainty through model averaging (Burnham and Anderson 2002).

To examine individual-level recruitment we analyzed observations of breeding males and females separately, as an offspring recruited into the breeding population could be counted for both parents and not represent two independent data points. We used a generalized linear model (GLM) in R 2.9.2 with a Poisson distribution and a log link to compare the number of fledglings to the number of those fledglings that were recruited. We used the same statistical procedure to examine the relationship between offspring fledged and the number of grandchildren recruited in the population. Offspring produced after 2007 were excluded from this analysis as they did not have adequate time to be recruited into the population, as it generally takes Swainson's Hawks at least 2 or 3 years to begin breeding (Woodbridge et al. 1995a).

We again used a GLM to examine the relationship between the average annual reproductive success (AARS) of each adult individual and the number of recruits it produced. AARS was measured as the mean number of offspring fledged for each individual divided by the number of breeding attempts we witnessed for that individual when its nest was located. We used both number of recruits and its quadratic to examine nonlinearities in the relationship between AARS and number of recruits. Similarly, we used a GLM to examine the relationship between AARS and the number of grandchildren produced. Results are reported as mean ± SE.

RESULTS

Over the course of this study we trapped and color-banded 248 (127 male, 121 female) adult Swainson's Hawks. In this population, the average span of an individual's known reproduction is 6.0 ± 0.32 years. We recorded 1101 fledglings produced in the study area; of those, 1050 were banded and 118 were recruited into the population. Twenty-five individuals had a known

grandmother. On average, individuals produced 4.10 ± 0.30 fledglings, 0.46 ± 0.07 recruits and 0.10 ± 0.02 grandchildren from those recruited fledglings over the course of their lifetime. Relatively few individuals accounted for a disproportionate number of fledglings produced by the population, with most individuals producing few or no fledglings (Fig. 1). The 121 females that were color marked are known to have produced 673 young, and 60 of those fledglings were recruited into the local breeding population. There was no difference between males (5.38 ± 0.29 years) and females (4.90 ± 0.48 years) in age at which we detected recruitment. Only one individual was excluded from the analysis, as it was caught late in the breeding season and could not be associated with a territory and showed no signs of breeding.

Results from the MARK analysis demonstrated that models including age at which individuals were recruited were the most appropriate (Table 1, $n = 949$, $\Sigma w_i = 0.998$) and that models including variation by cohort and year ($\Sigma w_i = 0.002$ and $\Sigma w_i = 0.000$, respectively) performed poorly. The best model predicted a quadratic trend in the age of recruits (Fig. 2). Only the age at recruitment being well supported indicates that the number of individuals produced each year was well correlated with the number of those individuals that were recruited into the breeding population (Fig. 3). Neither of our group covariates was well correlated with the probability that an individual would be recruited into the breeding population (Table 1). There were no problems with overdispersion, as $\hat{c} = 0.89$. Therefore we kept $\hat{c}$ at 1, as the consequences of $\hat{c} < 1$ are unknown. However, changing $\hat{c}$ to 0.89 did not change our models' order and therefore did not alter our conclusions.

The GLM of lifetime reproductive success and number of offspring recruited demonstrated that the number of chicks banded per adult over its lifetime is a highly significant predictor

TABLE 1.   Representative output results from program MARK. We created 24 models, with 8 of each of time, age, and cohort. All models have a recapture rate based on effort, and adult survival included linear and quadratic trends. The age models indicate that transition probability was varied by age, and the number indicates the grouping (e.g., age 3 indicates that transition probability was tested as age in 3rd-year age groups). T and T^2 indicate a trend and its quadratic, respectively. Total offspring produced was the number of offspring observed successfully fledged within the study area in each year. Average offspring produced was the average number of offspring observed per nesting attempt in each year.

Transition parameter	ΔAIC_c [a]	w_i	K [b]	Deviance
Age ($T + T^2$)	0	0.43	12	889.45
Age (3)	0.76	0.29	13	888.17
Age (2)	0.90	0.27	13	888.31
Age ($T + T^2$) + cohort (3)	14.51	0.00	18	891.67
Age ($T + T^2$) + time ($T + T^2$)	15.07	0.00	12	904.52
Total offspring produced	105.30	0.00	11	1942.12
Average offspring produced	105.80	0.00	11	1952.36

[a] AIC_c value for the top model was 102.4.
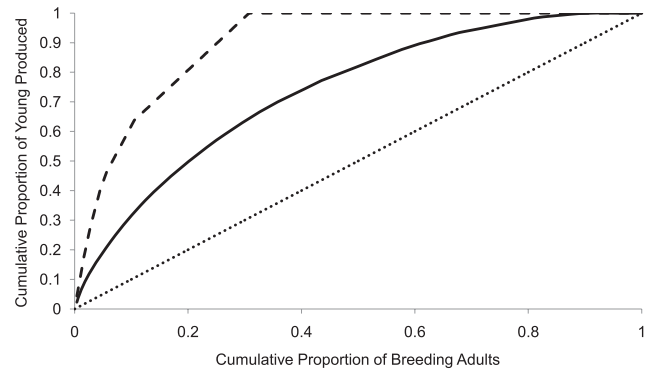[b] Number of parameters.

FIGURE 1.   Individual variation in total fledgling production among 310 color-marked Swainson's Hawks breeding between 1979 and 2007 in Butte Valley, California. While 221 (95%) adults successfully fledged young (solid line), only 75 (31%) recruited offspring into the local breeding population (dashed line). The dotted line shows the 1:1 line, where each individual would produce the same number of fledglings.
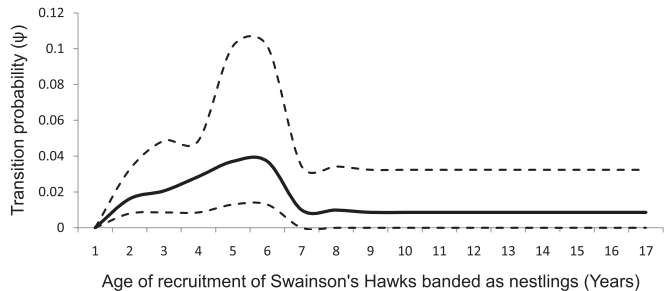

FIGURE 2.   Model-averaged transition probability of Swainson's Hawks banded as nestlings and recruited into the population according to age with 95% confidence intervals (dashed lines). Transition probability combines both survival of a pre-breeder and the probability that an individual returns to the local breeding population.
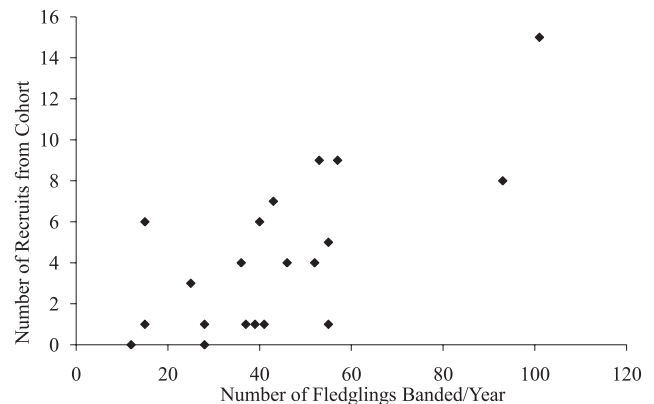

FIGURE 3.   The number of Swainson's Hawk recruited from each cohort compared to the number of fledglings banded in that cohort, 1979–2007.

of the number of recruits an individual generates for both males ($P < 0.0001$, df = 87) and females ($P < 0.0001$, df = 84; Fig. 4). Similarly, the number of chicks banded per adult over the course of its lifetime was significantly correlated with the number of grandchildren produced for both males ($P < 0.0001$, df = 87) and females ($P < 0.0002$, df = 84; Fig. 5, Table 2).

The GLM comparing AARS and number of offspring recruited demonstrated a quadratic trend in recruitment, where individuals with moderate reproduction in any given year generated higher number of recruits, both females ($P < 0.02$, df = 113; Fig. 6A) and males ($P < 0.001$, df = 131). In addition, AARS was positively correlated with number of grandchildren recruited for both females ($P < 0.02$, df = 113; Fig 6B), and males ($P < 0.004$, df = 131).

DISCUSSION

Our observation that few individuals produced a disproportionate number of recruits is typical of avian populations (Clutton-Brock 1988, Newton 1989), and our results that a smaller proportion of individuals produce all recruited offspring is similar to results for the Northern Goshawk (Wiens and Reynolds 2005). High densities of prey within the study area (Whisson et al. 1999), relatively limited habitat surrounding the valley (Woodbridge 1991), and a high rate of natal fidelity allowed us to examine the assumption that lifetime reproductive success is a reasonable predictor of recruitment. In addition, the availability of territories and continued expansion of the population within the area throughout the study (Briggs 2007) have allowed us to forgo modeling density dependence, simplifying the assumptions in our models.

At the population level, models of transition probability varying by offspring age at recruitment accounted for the majority of model weight (Table 1). The poor performance of models incorporating time and cohort indicates that there were no large differences between the transition probabilities of different cohorts. If there were differences in the probability of recruitment between cohorts, those models should outperform the age-only models. Likewise, there were no large differences between years in the transition probability of Swainson's Hawks, including years when pesticides were known to have killed large numbers of Swainson's Hawks in their winter range in Argentina (Woodbridge et al. 1995b, Goldstein et al. 1999). At least at the scale at which we were able to measure differences in cohorts (i.e., 3-, 4-, and 5-year groups), we could not detect differences in the probability of different cohorts being recruited into the breeding population. If a group of cohorts were in better condition or if density dependence were changing the probability of recruitment over time, we would expect the cohort and time models to perform better in our analysis. However, because we had to constrain our estimation of cohort recruitment into groups of years we may not have been able to detect more subtle differences in cohort recruitment.

These results suggest that measuring population-level reproductive success is a reasonable predictor of future
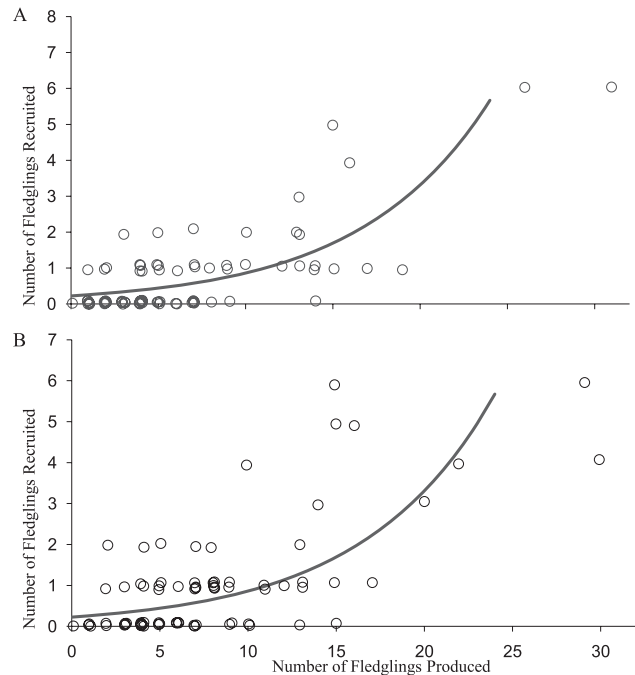

FIGURE 4.   Number of fledgling Swainson's Hawks from Butte Valley, California, produced per individual compared to the number of offspring recruited from those fledglings for males (A) and females (B). Each point represents an individual adult and lines represent the best fit based on a generalized linear model.
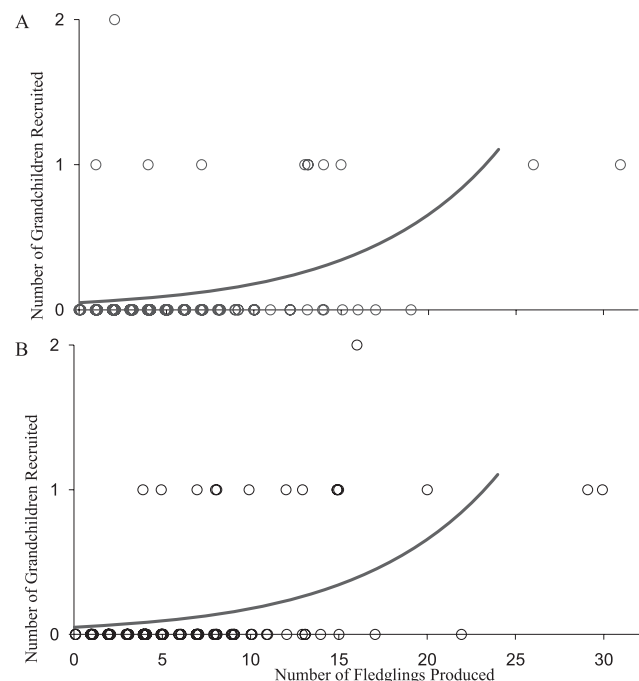

FIGURE 5.   Number of fledgling Swainson's Hawks from Butte Valley, California, produced per individual compared to the number of grandchildren recruited from those fledglings for males (A) and females (B). Each point represents an individual adult and lines represent the best fit based on a generalized linear model.
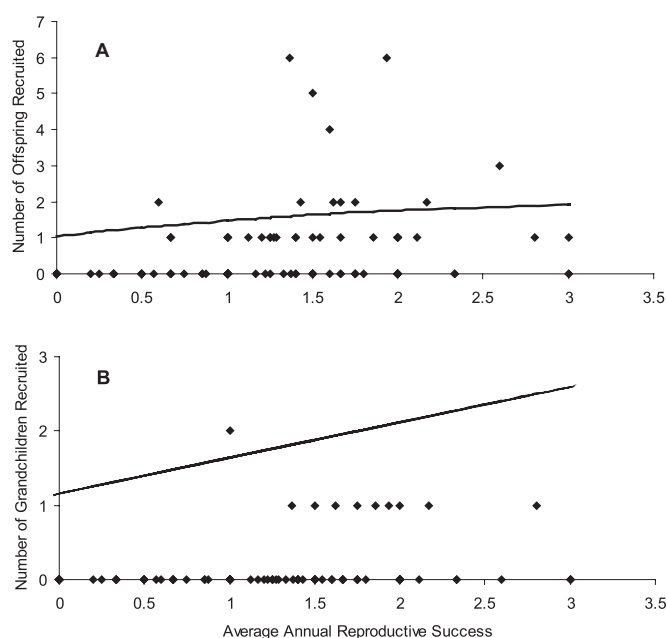
FIGURE 6.   Average number of fledglings produced per year for female Swainson's Hawks breeding in Butte Valley, California, compared to the number of offspring that individual recruited (A) and the number of grandchildren recruited (B). Each point represents an individual adult and lines represent the best fit based on a generalized linear model.

recruitment in this population. Because of low band recovery and recapture of prebreeders inside or outside of the study area, we were unable to separate survival of prebreeders and emigration rate and chose to lump them together in our estimates of transition probability, providing a single metric of probability of recruitment into the local breeding population. Our estimates of survival and recruitment (i.e., ψ) tend to be lower than those Schmutz et al. (2006) reported for another population of Swainson's Hawks in which annual survival of nestlings was between 0 and 1.

At the individual level, the GLM demonstrated that lifetime reproductive success was also a good indicator of recruitment at the next generation. Furthermore, the number of offspring fledged is significantly correlated with the number of grandchildren recruited into the breeding population. These data provide evidence that measuring lifetime reproductive success is a reasonable measure of future fitness.

Several previous studies have noted a high correlation between individual lifetime reproductive success and recruitment (e.g., Mills 1989, Sternberg 1989, Weatherhead and Dufour 2000, Wiens and Reynolds 2005). These results provide some support for many current protocols for avian population monitoring, particularly those in which the reproductive success of populations or the lifetime reproductive success of a species monitored. While stochastic factors can play an important role in any given reproductive attempt, lifetime

TABLE 2.   Reproductive values over the course of an individual Swainson's Hawk life from 1979 to 2007 in Butte Valley, California; n, number of individuals observed; fledglings, mean number fledglings produced over the course of an individual's life; recruits, average number of those fledglings recruited into the breeding population; grandchildren, average number of grandchildren an individual had recruited into the population.

	n	Fledglings	Recruits	Grandchildren
Males	127	6.09 ± 0.48	0.61 ± 0.11[a]	0.13 ± 0.03[a]
Females	121	5.61 ± 0.48	0.50 ± 0.10[a]	0.10 ± 0.03[a]

[a]Number of fledglings produced statistically significant at $P < 0.001$.

reproductive success and population-level reproductive success both provide a reasonable substitute for recruitment.

The average number of offspring produced was well correlated with number of offspring recruited; however, the relationship was not linear. In fact, individuals that produced a high number of offspring on average generally recruited comparatively few offspring. Individuals that produce >2 offspring per year on average have decreased adult apparent survival (Briggs et al., in press) and, therefore, likely make fewer reproductive attempts and their lifetime reproductive success is lower. Additionally, individuals that produce few offspring on average also generally have low offspring recruitment, as they would have low lifetime reproductive success and fewer opportunities to recruit offspring. In contrast, individuals producing an intermediate number of offspring have the potential to recruit the highest number of offspring. This is likely due to survival higher than for individuals whose average reproduction is higher and an ability to produce the largest number of offspring over a lifetime. Therefore, the best strategy is to produce moderate numbers of offspring. This is unsurprising given that long-lived species should favor survival over reproduction to maximize fitness in the face of a trade-off between the two measures (Stearns 1992). Similarly, the higher the average number of offspring produced the higher the number of grandchildren recruited. While we did not observe a similar quadratic relationship, limited sample sizes may have precluded our ability to detect that type of relationship.

Perhaps more importantly, this result provides evidence that conclusions concerning individual quality of long-lived species based on relatively short-term studies may not provide a reasonable estimate of individual quality. If studies examine estimates of individual quality based on only a few years of reproduction, the general conclusion is that individuals that produce the most offspring are of the highest quality (e.g., Hanssen et al. 2003). However, without understanding if and what trade-offs exist, average reproduction alone is likely to be a poor substitute for fitness.

We made several assumptions during this analysis. First, we assumed there was no bias in banding chicks of poor

versus high-quality individuals. This assumption was likely reasonable, as most individuals that successfully reproduced had their chicks banded, and banding was limited mostly by access to private land. We also assumed that density dependence was not a factor in this population because the number of territories increased through the study and there is still habitat seemingly available for additional territories to be established. However, we did test for density dependence by including both cohort size as well as average number of fledglings produced per nest in our analysis. Neither of those variables was well supported in our models, providing evidence there is not yet a problem with density dependence in this population. We assumed no bias in emigration of fledglings from the study area that arose because of differences in conditions at the nest sites (e.g., density dependence, poor condition). In fact, there is some evidence that dispersal distance can change due to natal conditions. For example, in the Great Tit (*Parus major*), Tilgar et al. (2010) found that individuals that fledged in coniferous forests dispersed farther than those fledgling in deciduous forests and males that were heavier as nestlings dispersed farther. However, our assumption of no bias in emigration was necessary because of low rates of encounter outside of the study area. In fact, only three individuals have been recovered outside the study area during the breeding season, and none had reached breeding age (B. Woodbridge, unpubl. data). Violations of this assumption could change the results and cause more complex relationships between lifetime or average annual reproductive success and recruitment. We also assumed no extra-pair paternity in the analysis of the numbers of recruits generated by males. This assumption may be invalid, given that extra-pair copulations were observed several times through the study; however, we have no data on the rate of extra-pair fertilization in Swainson's Hawk and no way to determine paternity post hoc. Finally, we assumed there was no difference in the primary sex ratio. A similar number of males and females was recruited into the study population (78 and 60, respectively). We cannot assess whether emigration rate, differences by sex in juveniles' and subadults' survival, or some combination of the two factors explains these differences if they are not the result of stochastic processes and reflect a real difference between the sexes.

This study supports current protocols of population monitoring but may apply only to populations that are increasing or in which effects of density dependence are limited. While survival of a long-lived species may be a better proxy for fitness than reproductive success, reproductive success may be a more cost-effective alternative, especially for short-term studies that may not provide information adequate to yield reliable estimates of survival (e.g., for long-lived, wide-ranging, or difficult-to-capture species). In this population of Swainson's Hawk, reproductive success is a reasonable measure of the number of individuals that will be recruited into the population.

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