Research Article

Correlates of Survival in Swainson's Hawks Breeding in Northern California

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ABSTRACT We used a 30-year study of breeding Swainson's hawks (*Buteo swainsoni*) in northern California to examine correlates of adult apparent survival using multistate models in Program MARK. Specifically, we examined age-related patterns in adult apparent survival and how adult survival was correlated with average annual nest productivity, annual reproductive output, western juniper (*Juniperus occidentalis*) density around nest sites, distance to agriculture, and amount of agriculture within a territory. Annual estimates of adult survival varied from 0.85 to 0.9 (SE = 0.02). There were no indications of senescence or other patterns of age-related changes in adult apparent survival. Adult survival was inversely correlated with average reproductive output, with individuals producing >2 offspring having decreased survival, reflecting a possible trade-off between reproduction and survival. Conversely, reproduction in any year was positively correlated with survival, providing evidence of individual quality influencing adult survival. The distance an individual had to travel to agriculture, where most individuals forage, was negatively related to survival. Primary productivity within the average Swainson's hawk territory was positively correlated with adult survival. Our results indicate that individuals may have higher survival and fitness in areas with high proportions of irrigated agriculture that provides high prey densities, particularly alfalfa. © 2011 The Wildlife Society.

KEY WORDS *Buteo swainsoni*, reproduction, survival, Swainson's hawk, trade-off.

Swainson's hawks (*Buteo swainsoni*) are medium sized (700–1,300 g) migratory raptors that nest throughout much of western North America, exhibiting a slow life history pattern (i.e., K-selected), with high survival, low reproductive rates, and delayed reproduction (Pianka 1970). There was considerable attention on the population dynamics of Swainson's hawks when mass mortalities were discovered in Argentina, a result of pesticides used to control grasshopper outbreaks (Woodbridge et al. 1995; Goldstein et al. 1996, 1999*a*). These mortalities likely represented a loss of as much as 5% of the global Swainson's hawk population (Goldstein et al. 1999*b*). Like many grassland species (e.g., Brennan and Kuvlesky 2005, With et al. 2008), Swainson's hawk populations have declined in some portions of their range (Bloom 1980, Littlefield et al. 1984, Herron et al. 1985). Despite these declines, little is known about correlates of adult survival in Swainson's hawks, which is likely the most important parameter in determining a population growth rate (λ; Heppell et al. 2000, Saether and Bakke 2000, Ricklefs and Wikelski 2002, Stauss et al. 2005). Our goal was to examine both intrinsic and extrinsic variables that could affect adult survival in Swainson's hawks.

Intrinsic variables (e.g., trade-offs, individual quality, experience) are likely important determinants of an individual's performance (e.g., Ricklefs 2000, McCleery et al. 2008). For example, investment in reproduction may influence survival as increasing reproductive output may diminish an individual's reserves and decrease probability of future survival (Stearns 1992, Roff 2002). Similarly, adult survival has been shown to change with individual's age in a number of wild populations (Williams et al. 2006). For example, adult survival of sparrowhawks (*Accipiter nisus*) increases initially and then declines in the oldest age classes as individuals senesce (Newton et al. 1997).

Extrinsic factors (e.g., nest habitat, competition, predation pressure, rainfall) could similarly affect population parameters. Such factors have been the focus of intense research for decades (e.g., Horak and Lebreton 2008), and relationships between population parameters and habitat characteristics have been particularly well studied in many species. Habitat characteristics around Swainson's hawk nests may influence survival by exposing individuals to greater predation, competition, or decreased food supplies. Dense stands of western juniper (*Juniperus occidentalis*) have encroached on large portions of our study area and may provide poor nesting habitat for Swainson's hawks (Woodbridge 1991, Janes 1994).

The distance individuals travel to foraging areas also may influence reproductive costs by increasing energetic demands (Stauss et al. 2005). In the Butte Valley, California, irrigated

alfalfa (*Medicago sativa*) is the predominate crop type and is highly favored for foraging by Swainson's hawks due to high prey densities (Woodbridge 1991, Whisson et al. 1999, Brown et al. 2008). Irrigation of alfalfa keeps small mammal densities consistent between years. Our objectives were to 1) examine age-related changes in apparent survival in Swainson's hawks and 2) identify other covariates of adult apparent survival of Swainson's hawks.

STUDY AREA

We conducted our study in the Butte Valley in north central Siskiyou County, California, USA (415 km^2; 41° 49′N, 122° 0′W). Butte Valley was part of the Basin and Range Physiographic Province, and its soils, topography, and vegetation were typical of this province (Franklin and Dyrness 1973). Butte Valley ranged from 1,280 m to 1,340 m in elevation and was approximately 415 km^2 (Woodbridge 1991). Climate was typical of the mountain west, with warm, dry summers and cold, snowy winters. Mean annual precipitation during our study was 33.1 cm, ranging from 23.0 cm to 50.0 cm (C. Cheyne, Klamath National Forest, unpublished data).

Vegetation in the Butte Valley consisted of approximately 21% sagebrush steppe, 22% juniper woodland, and 55% agricultural land (Woodbridge 1991). Irrigated alfalfa was the primary crop type in the valley. Grains comprised most of the other crops, with potatoes, strawberries, carrots, and green onions composing a smaller fraction, depending on the year. Large concentrations of Belding's ground squirrels (*Spermophilus beldingi*) and voles (*Microtus* spp.) occurred in some agricultural types, notably irrigated alfalfa. Densities of up to 296 ground squirrels/ha have been estimated in the study area (Whisson et al. 1999), providing an abundant prey source for Swainson's hawks. Low prey densities outside the study area likely explained a much lower density of nesting Swainson's hawks outside the study area (Woodbridge 1991). Therefore we focused our efforts in Butte Valley and neighboring Red Rock Valley (41° 45′ 42″N, 121° 48′ 22″W).

METHODS

Data Collection

Surveys for Swainson's hawks began in Butte Valley in 1979. From 1979 to 1986 survey effort was focused on areas in and around the Butte Valley National Grasslands, about 35% of the current study area. We trapped and marked breeding adults with unique plastic numeric color bands to individually identify each bird; we banded nestlings with United States Geological Survey (USGS) metal bands. We trapped adult hawks using a dho-gaza with a great-horned owl (*Bubo virginianus*) lure (Bloom et al. 1992) or bal-chatri with a mouse or sparrow lure. In 1987, we expanded surveys to include the entire valley floor and neighboring Red Rock Valley to attempt to provide a complete census of the local breeding population (hereafter, population). We defined the population as including any individual breeding within the Butte or Red Rock Valleys and we monitored the population

intensively through the late 1990s. Survey effort varied from 1999 to 2009 because of variation in the number and experience of field technicians, however, the high visibility of the hawks permitted observation of most marked adults. Each year, we attempted to read all color bands within the study area. Whenever possible we also read USGS aluminum bands for individuals without color bands if individuals could not be trapped. Despite our attempts to census the entire population there were likely nests that were not located each year because of private land restrictions or because nests failed early in the nesting season (Mayfield 1961).

We observed adults during the breeding season for signs of mating behavior (e.g., undulating flight, copulation, nest building). We surveyed the valley floor by truck and by foot from mid-April through August. High road densities, facilitated by the agricultural nature of the valley, allowed us to conduct much surveying from vehicles, which reduced disturbance to breeding pairs. Once we identified pairs we observed them until we located nest sites or the individuals were lost (e.g., by soaring too high). We monitored traditional sites until we found a nest or until investigators were confident that there was no activity at the site. We did not approach nest trees until at least a week after the mean hatching date (16 Jun) to reduce the potential for chilling eggs or nest abandonment (Woodbridge 1991). We recorded the number and approximate age of nestlings whenever possible; we banded nestlings when they reached approximately 3 weeks of age. We recorded nest sites on 1-m resolution digital ortho-quarter quadrangles (DOQQs) and later input them into a Geographic Information System (GIS; ArcMAP, version 9.0). All procedures were approved by the Institutional Animal Care and Use Committee at the University of Nevada, Reno (IACUC approval no. 00115).

Data Analysis

We began by investigating age-related changes in adult apparent survival. Therefore we limited the first analysis to individuals originally banded as nestlings and later returned to the study population as breeders. Several individuals lost color bands during the study, violating one of the assumptions of Cormack–Jolly–Seber models. Loss of color bands may cause individuals to disappear from the sample, unless recaptured, negatively biasing apparent survival estimates. Therefore we used multistate models as implemented in Program MARK (Burnham and White 1999) to account for loss of plastic color bands (Brownie et al. 1993, Conn et al. 2004). We first investigated age-related changes in adult apparent survival using a total of 3 states, 2 breeding states and an unobservable nonbreeding state. The first breeding state was for individuals with a unique color band in addition to the USGS aluminum band, which allowed ready individual identification. The second breeding state was for individuals that had lost the color band and would likely have lower encounter probability (i.e., probability of reading a band or trapping an individual). We used the MLogit link to constrain the 2 breeding states transition probabilities (i.e., probability that an individual loses a color

band or is recaptured and given a second color band) to equal one. Our third state was an unobservable nonbreeder state for individuals prior to being recruited into the breeding population. Nonbreeders were individuals banded as nestlings and transitioned to breeders once they returned to the study area to breed; we considered them breeders once we observed them defending territories, mating, or nest-building. Once we considered them a breeder they could not transition back to a nonbreeder (i.e., we set transition probability from breeder to nonbreeder to zero). Although it is possible that an individual may have bred elsewhere prior to arrival in our study area, we cannot assess the likelihood of this occurring. As most breeders were trapped using a dho-gaza and great-horned owl, trapping of transient (i.e., individuals that were just moving through the study area) or floaters (i.e., individuals that were not breeding on the study area) was minimal. However, because we were not likely to capture transient or breeder individuals, we could not include them in the analysis and they did not affect our results. We identified with a mate or offspring those individuals trapped away from the nest on a bal-chatri style trap (Bloom et al. 1992) to ensure they were associated with a given nest. We constrained survival to 1.0 for the first 2 years, as we saw no marked individual in the study area before age 2 years, and individuals needed to survive until at least that point to be included in the analysis. We first modeled transition probability as a function of individual age, with constant recruitment after 6 years.

Next we modeled encounter probability. First, we set encounter probability of nonbreeding individuals to zero, as we only observed breeding individuals within the study area. Encounter probability differed between the 2 breeding states to account for differences in detection rates due to differential survey efforts between years. We classified survey effort into 3 categories based on number and experience of technicians: incomplete, moderate, and intense. During incomplete surveys (i.e., 1979–1986) we surveyed only a portion of the valley, minimizing the number of territories and color banded adults being monitored. We allowed for variation with sex, time, survey effort, and interactions of these variables. We also examined correlates with juniper density around the nest site to determine if individuals nesting in less open (i.e., less conspicuous) habitats would have decreased detection rates.

For adult apparent survival we examined models of time, age, and linear and quadratic trends in both age and time. We also grouped age in 2- to 5-year intervals to obtain more precise statistical estimates of parameters. We selected models using Akaike Information Criterion adjusted for small sample sizes (AIC_c, Akaike 1973), and we used sums of weights for all models containing each parameter to evaluate evidence for each term (Burnham and Anderson 2002).

Once we modeled the effects of known-aged individuals, we examined apparent survival of all adults trapped in Butte Valley using multistate models in Program MARK. We used multistate models again to account for loss of color bands. We calculated transition probabilities for individuals transitioning from having a color band to not having a color band

and the transition probability from not having a color band (after having previously had a color band) to getting a color band (i.e., the probability of being retrapped). We modeled transition probability first and selected the most parsimonious model. We examined sex, age of the color band, and time since losing the color band to determine if age of the band played a role in its loss. We modeled encounter rates in the same manner as the previous model.

Once we optimized transition probability and encounter rate, we examined variation in adult apparent survival. We allowed apparent survival to vary by sex, year, state, and interactions with all covariates. We also used linear and quadratic temporal trends in year to account for previously described declines in apparent survival during the mid-1990s in association with pesticide-induced mortality events in South America (Briggs 2007).

For each year we input nest locations into ArcView 9.0 and calculated several variables from grayscale 1-m resolution digital ortho-quarter quads (DOQQs), including number of junipers within a 25-m radius of the individuals nest sites, average distance to agriculture, and average area of agriculture within 500 m of an individual's nest site. We chose 500 m from the nest site, as this was the estimated average territory size in our study area based on nearest-neighbor distances (Woodbridge 1991). We measured juniper density using Feature Analyst (Visual Learning Systems 2002) on the DOQQs. Feature Analyst is a trainable GIS program that iteratively selects features based on parameters the user sets. We buffered nest sites and used Hawth's Analysis Tools in ArcGIS 9.0 to count the number of junipers within a 25-m radius of the nest site. We manually digitized agricultural areas using 1-m resolution DOQQs. We did not identify differences between agricultural types due to the lack of temporal resolution of the DOQQs. Although there has been limited expansion of agriculture within the study area (C.W. Briggs, University of Nevada, Reno, unpublished data), change appears to be limited to 2 areas of the valley and would affect only 4–5 territories out of >100 observed in the last several years of the study.

We also used average annual nest productivity (AANP) of an individual from all known breeding attempts and number of fledglings produced each year by each individual. We calculated AANP for each individual for all years we observed it, and AANP was simply the average known fledgling output of an individual. If an individual's nest was not located in a given year, we gave it the mean AANP for that year for each time varying covariate ($n = 19$). By giving missing individuals the mean number of fledglings for a year we ensured that those individuals whose nests we did not locate could not overly influence our estimates of the influence of reproduction on apparent survival (i.e., provide a conservative estimate of reproduction on apparent survival). In contrast, the number of fledglings produced each year was a time-varying covariate in our model reflecting the reproductive output for each year we observed the individual.

We included the covariates iteratively, creating models with a combination of each variable, until we discovered the most parsimonious model. We used AIC adjusted for

small sample sizes and overdispersion (i.e., QAIC$_c$) to rate candidate models and create model weights representing the relative likelihood of each candidate model (Burnham and Anderson 2002). We considered models with the lowest QAIC$_c$ to be best supported (Burnham and Anderson 2002). We calculated model weights to provide an index of likelihood for each candidate model. We can assess the relative strength for each model term (e.g., sex) by summing the weights of all models containing a particular term to calculate each terms relative importance (RI). We used Program U-Care (Choquet et al. 2005) to examine problems with overdispersion in the data (ĉ, Pradel et al. 2005). Testing for overdispersion ensures that the dataset meets the assumptions of equal survival and resight ability among groups in mark-recapture data. A ĉ of >1 indicates there are problems with overdispersion, and adjustments should be made.

RESULTS

From 1979 to 2009, we trapped and marked 310 breeding adults (M = 159, F = 151); 21 were known to have lost a color band. We observed 40 ± 4.0 nesting attempts over the course of the study, with the number of nests found generally increasing linearly over the course of the study (Briggs 2007) from 6 in 1979, 31 in 1987 when we began the census to 86 in 2009. The oldest individual observed was 24 years old (Houston 2005), and we observed individuals an average of 4.2 ± 0.2 years. Average annual nest productivity was ($\bar{x} \pm$ SE) 1.05 ± 0.04 (range 0.0–4.0), and annual reproduction ranged from 0.42 ± 0.12 in 2000 to 2.04 ± 0.16 in 1994. There was no evidence of overdispersion in the dataset of known-aged individuals. Based on our analysis of known-aged individuals there was no evidence for changes in age-related apparent survival ($n = 95$, sum of model weight, RI = 0.001, Table 1) or for differences in apparent survival between the sexes (RI = 0.001). Instead, models indicating trends in apparent survival were the most parsimonious models (RI = 0.999, Table 1), therefore we did not examine age in models of the entire population. Encounter rate was best predicted by survey effort.

Apparent survival of the study population changed during the study, ranging from 0.85 to 0.90 (SE = 0.02), corresponding to what has been previously reported (Briggs 2007). Again, there were no differences between sexes in apparent survival (RI = 0.001). The dataset of all trapped adults showed some evidence of being overdispersed, and we adjusted ĉ to 1.1 to account for the overdispersion. All top ranked models contained both linear and quadratic trends to account for decreased apparent survival in the mid-1990s (Table 2). Encounter rates varied with survey effort for both states. Among color-banded individuals, encounter rates ranged from 100% during early years of the study, when there were fewer individuals to locate and only part of the study area was trapped, to 67.6% ± 4.7% when we conducted moderate surveys. Among individuals that lost their color bands, encounter rates varied from 4.6% ± 1.8% in years of incomplete surveys, to 30.2% ± 6.0% during years of intense surveys. Juniper density was not related to encounter rates.

Transition probability from being color-banded to losing the color band was lower in the first year after they received a band (14.4% ± 7.8%) than in subsequent years (28.5% ± 2.6%; RI = 0.998). There also was evidence that recapture of the individual (i.e., transition from unbanded to banded again) was constant at 13.8% ± 2.0%.

All top models contained linear and quadratic trends in apparent survival to account for previously described patterns in adult apparent survival (Briggs 2007). Average annual nest productivity (mean 1.05 ± 0.79 fledglings/year) and its quadratic were strong predictors of apparent survival (RI = 1.0 and RI = 1.0, respectively; Table 1). As AANP increased past 2 fledglings/year, model-averaged apparent survival was negatively impacted (Fig. 1). In contrast, the number of fledglings produced per year was positively correlated with model-averaged apparent survival (Fig. 2).

Distance to agriculture (487 m ± 53 m) and the amount of agriculture (0.20 km^2 ± 0.02 km^2) around a nest site were important predictors of apparent survival (RI = 0.67 and 0.84, respectively). Distance to agriculture was negatively correlated with apparent survival (Fig. 3). Amount of agriculture within a territory was positively correlated with apparent survival (Fig. 4). There was slight evidence for lower apparent survival in areas of high juniper density (RI = 0.13).

Table 1. Model selection for models of adult apparent survival from known-aged Swainson's hawk individuals ($n = 95$), Butte Valley, California, 1979–2009 calculated using multistate models in Program MARK.

Model	ΔQAIC$_c$[a]	w_i[b]	Model likelihood	K[c]
T[d] + T^2	0.0	0.97	1.00	6
T	7.0	0.03	0.12	5
Age 4[e]	13.9	0.0	0.00	9
Age 3[f]	20.3	0.0	0.00	12
Null	56.2	0.0	0.00	4

[a] ΔQAIC$_c$, difference between the quasi-likelihood version of Akaike's Information Criterion of a model and the best performing model.

[b] w_i, Akaike model wt.

[c] K, no. of parameters used in the model.

[d] T, annual temporal trend.

[e] Age 4, survival models accounting for age of individual is binned in 4-yr increments (i.e., individuals with ages 3–6 yr, 7–10 yr, etc. are constrained to the same survival estimate).

[f] Age 3, survival models accounting for age of individual is binned in 4-yr increments (i.e., individuals with ages 3–5 yr, 6–8 yr, etc. are constrained to the same survival estimate).

Table 2. Representative models for multistate models of apparent annual survival from marked Swainson's hawk individuals ($n = 310$), Butte Valley, California from 1979 to 2009 calculated using multistate models in Program MARK. Recapture probability was related to survey effort and whether an individual had a color band. All models listed contain linear and quadratic annual temporal trends previously described (Briggs 2007).

Model	$\Delta QAIC_c$[a]	w_i[b]	Model likelihood	K[c]
AANP[d] + AANP^2 + AgA[e] + AgD[f] + annualRS[g]	0.00	0.37	1.00	18
AANP + AANP^2 + AgA + annualRS	0.29	0.32	0.87	17
AANP + AANP^2 + AgA + AgD + Jun[h] + annualRS	2.06	0.13	0.36	19
AANP + AANP^2 + AgD + annualRS	2.34	0.12	0.31	17
AANP + AANP^2 + AgD + AgD^2 + annualRS	4.32	0.04	0.12	18
AANP + AANP^2 + AgA + AgD + annualRS	8.46	0.01	0.01	16
Null	53.95	0.00	0.00	13
Jun	55.97	0.00	0.00	14

[a] $\Delta QAIC_c$, difference between the quasi-likelihood version of Akaike's Information Criterion of a model and the best performing model.
[b] w_i, Akaike model wt.
[c] K, no. of parameters used in the model.
[d] AANP indicates average annual nest productivity (i.e., number of fledglings produced) for an individual during the study.
[e] AgA, amount of agriculture within a 500-m radius of the nest site.
[f] AgD, distance from a nest site to the nearest agricultural field.
[g] annualRS, time-varying covariate of number of offspring produced in a given year.
[h] Jun, juniper count within 25 m of the nest site.

DISCUSSION

We did not expect to see a strong trade-off between annual reproduction and adult apparent survival because of the aforementioned life history trade-offs and because Swainson's hawks demonstrate brood reduction (Pilz and Seibert 1978; Bechard 1983). Therefore individuals would only produce the number of chicks they could afford to provision based on the resources available. However, our results provide evidence that although a few high-quality
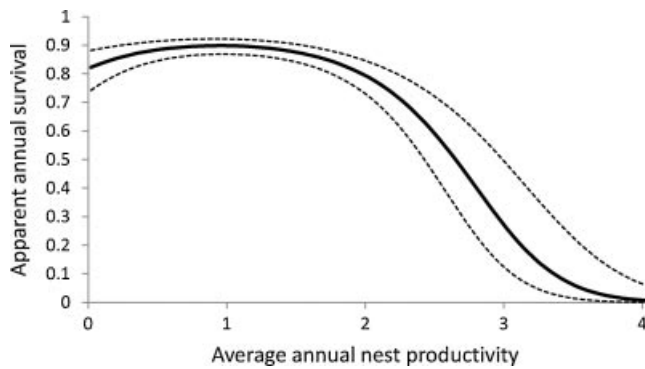

Figure 1. Relationship between model averaged apparent annual adult survival rate and average annual nest productivity of Swainson's hawks ($n = 310$) in Butte Valley, California, 1979–2009 calculated using multistate models in Program MARK.
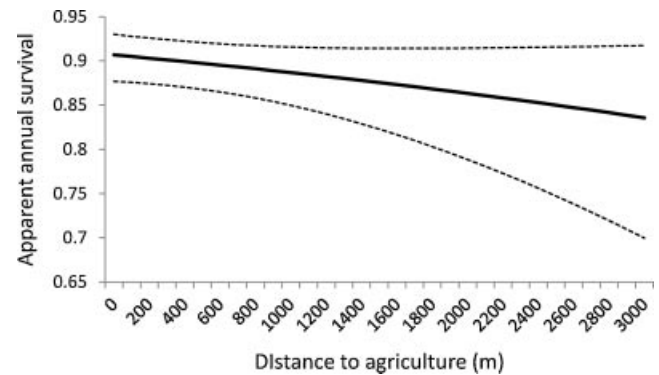

Figure 3. Relationship between apparent annual adult survival rate and distance from an individual's nest to the nearest agricultural field of Swainson's hawks ($n = 310$) in Butte Valley, California, 1979–2009 calculated using multistate models in Program MARK.
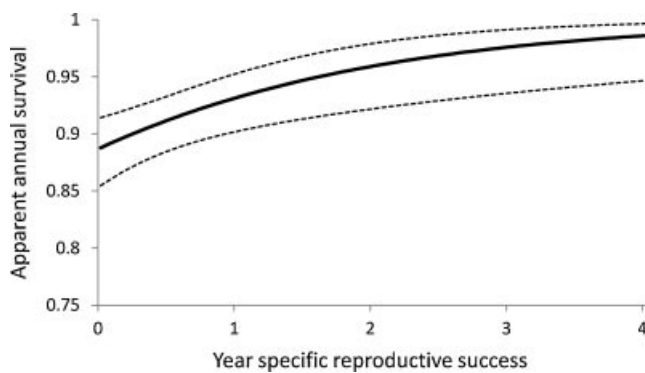

Figure 2. Relationship between model averaged apparent annual adult survival rate and year-specific nest productivity of Swainson's hawks ($n = 310$) in Butte Valley, California, 1979–2009 calculated using multistate models in Program MARK.
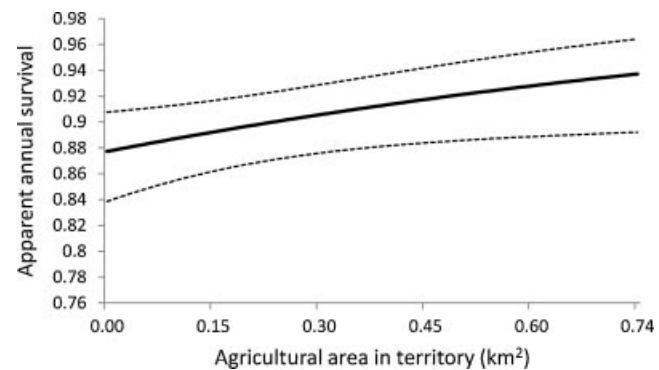

Figure 4. Relationship between model averaged apparent annual adult survival rate and amount of agriculture (km^2) within the average territory of Swainson's hawks ($n = 310$) in Butte Valley, California, 1979–2009 calculated using multistate models in Program MARK. Average territory size was 785,000 m^2 (Woodbridge 1991).

individuals are capable of producing more offspring over time (e.g., 30% of individuals produce 65% of all fledglings produced; Briggs 2007), there are tradeoffs between reproduction and apparent survival at the population level. We found that AANP of an individual was a strong predictor of apparent survival; increasing nest productivity >2 fledglings/year on average was associated with decreased apparent survival. Although there was little variation in apparent survival associated with producing between zero and 2 fledglings per year, there was a steep decline in apparent survival associated with producing an increased number of fledglings. As a long-lived species, Swainson's hawks should maximize apparent survival at the expense of current reproduction (Stearns 1992). Individuals that consistently fledge >2 offspring appear to experience a trade-off in the form of decreased apparent survival. Based on these results we would expect for individuals to maximize longevity, and therefore reproductive value, average reproduction to be approximately 2 fledglings per year on average (Fig. 1). If individuals produce substantially more than 2 fledglings per year on average apparent survival starts dropping rapidly. Interestingly, the average number of fledglings produced when a nest successfully produces offspring is 2.01 across all the years of our study. However, this number is likely dependant on average prey resources found within the population. In contrast to AANP, annual reproduction was positively correlated with apparent survival, providing evidence for individual quality (Fig. 2). We define individual quality as individuals with higher fitness, either due to higher intrinsic survival rates, increased reproduction, or some combination that allows for increased reproduction over an individual's lifetime. Those individuals that can produce a high number of fledglings are likely individuals in good territories with high prey abundance, incurring low costs for increasing reproduction. Although 2 offspring per reproductive attempt seems to be the cut-off in our study area, this may change depending on habitat characteristics. For example, in areas with lower prey abundance or availability, breeding individuals may not be able to produce at such high rates without incurring survival costs.

Annual trade-offs between reproduction and survival has been observed experimentally in several species (e.g., Dijkstra et al. 1990, Daan et al. 1996, Golet et al. 1998). Increasing reproductive costs appears to reduce future survival and could reduce fitness in long-lived species (Stearns 1992). However, to our knowledge average nest productivity over an individual's lifetime has not been examined in relation to survival. Annual reproduction in any given year may not limit apparent survival because when prey is abundant individuals may not experience long-term costs when producing >2 young. However, consistently producing >2 offspring would likely result in individuals experiencing poor conditions in a temporally variable environment. Therefore, our measure of AANP may reflect individuals that overproduce during years of poor prey abundance and incur reproductive costs that subsequently influence apparent survival. Unfortunately we cannot assess the number of nestlings initially produced in a given nest attempt and any possible brood reduction because we often did not check nests until chicks were several weeks old to avoid researchers causing nest abandonment.

Juniper density around the nest site was not strongly correlated with apparent survival. Individuals nesting in areas of high density juniper did not have a lower apparent survival probability, indicating that potential increases in competition (Janes 1994) or predation did not negatively affect apparent survival. This lack of a correlation should not be interpreted to mean that encroachment of junipers in sagebrush dominated systems has no effect on population dynamics of Swainson's hawks, as juniper woodland provides poor foraging opportunities and is rarely used by foraging individuals (Woodbridge 1991).

Both distance to agriculture and amount of agriculture in a territory were good predictors of apparent survival for Swainson's hawks. Swainson's hawks in our study area forage primarily in agricultural areas, notably alfalfa, and will travel up to 10 km to forage in alfalfa fields (Woodbridge 1991). Individuals that nested farther from agriculture had decreased nest success (Fig. 3), suggesting that the further individuals had to travel to capture prey the greater the energetic costs incurred. Alternatively, individuals that nested farther from agriculture may have been competitively excluded from the best foraging areas by other nesting Swainson's hawks or red-tailed hawks (*Buteo jamaciensis*). Similarly, the amount of agriculture in a territory was positively correlated with annual apparent survival (Fig. 4). Increased agriculture (particularly alfalfa) likely provides increased foraging opportunity and capture success, allowing individuals to spend less time foraging and more time engaged in activities that enhance survival (e.g., caloric intake, resting, ectoparsite removal).

Despite these observed relationships, we were unable to separate the effects of individual quality from any of our habitat variables. Individuals of poorer quality may be relegated to territories that are farther from foraging areas or have less high quality foraging habitat. Therefore the observed relationships between apparent survival and agriculture may be caused by competition among individuals of varying quality rather than costs associated with reproduction. Future work is needed to determine if reproductive costs or individual quality is driving these patterns.

We found no evidence of senescence or other age-related apparent survival differences in apparent survival of adult Swainson's hawks, in contrast to some other long-term studies of birds (e.g., Newton et al. 1997). However, the long-lived nature of Swainson's hawks and our small sample sizes of known-aged individuals may limit our ability to detect changes in survival of the oldest age classes. Additionally, our study occurred for only a few years longer than the oldest known Swainson's hawk (Houston 2005), meaning that few individuals have been able to reach the oldest age classes. In fact, in the 2010 field season, we observed 3 additional individuals as breeders that tied the longevity record for Swainson's hawks (C. Briggs, unpublished data). Therefore further study may be necessary to adequately address questions of senescence.

We note that as with all studies of apparent survival it is impossible to determine the number of individuals that moved from the study area. However, our results provide evidence of high adult apparent survival in Swainson's hawks, and are similar to those previously reported for an Alberta population of Swainson's hawks (survival = 0.843; Schmutz et al. 2006). There was one sighting of a breeding individual moving from Red Rock Valley to Butte Valley during the study, a movement of 13.25 km. However, we have no information on movement rates outside the study area. It has long been known that emigration from the study population will bias survival estimates low. Therefore lower reproduction may be correlated with lower apparent survival if breeding failure is correlated with an individual's propensity to move to a new territory and subsequently leave the study area.

MANAGEMENT IMPLICATIONS

Swainson's hawks are listed as threatened in California and experienced as much as a 90% decline from 1900 to 1979 (Bloom 1980). With multiple threats, such as agricultural conversion (Estep 1989, Brown et al. 2008, Swolgaard et al. 2008) and development of wind energy it is prudent to provide estimates of apparent survival from healthy populations. As the population in our study area expanded during our study (Briggs 2007), it can provide a reasonable baseline for managers assessing California Swainson's hawk populations. Although enhancing survival of buteos may be difficult, it is still likely the most important demographic parameter controlling the growth of this population (Saether and Bakke 2000). Changing land-use practices within the study area and in many parts of California, particularly conversion to row crops and other poor foraging habitat, has the potential to limit recovery of Swainson's hawk populations in California (Brown et al. 2008). Therefore modeling of species that nest in agricultural matrices needs to account for not only changes due to management action, but also need for potentially shifting agricultural markets.

ACKNOWLEDGMENTS

LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kaido, Budapest, Hungary.

Bechard, M. J. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. Wilson Bulletin 95:233–242.

Bloom, P. H. 1980. The status of Swainson's hawks in California. Pages 42. California Department of Fish and Game Federal Aid in Wildlife Restoration Project, Sacramento, USA.

Bloom, P. H., J. L. Henckel, E. H. Henckel, J. K. Schmutz, B. Woodbridge, J. R. Bryan, R. L. Anderson, P. J. Detrich, and T. L. Maechtle. 1992. The dho-gaza with great horned owl lure: an analysis of its effectiveness in capturing raptors. Journal of Raptor Research 26:167–178.

Brennan, L. A., and W. R. Kuvlesky, Jr. 2005. North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management 69:1–13.

Briggs, C. W. 2007. Survival and nesting ecology of Swainson's hawks in Butte Valley, CA. Thesis, University of Nevada, Reno, Reno, USA.

Brown, J. L., C. W. Briggs, and M. W. Collopy. 2008. Swainson's hawk nesting habitat and patterns of expected land-use change. Great Basin Birds 10:16–25.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

Burnham. K. P., and D. R. Anderson, 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burnham, K. P., and G. C. White. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Choquet, R., A. M. Reboulet, J. D. Lebreton, O. Gimenez, and R. Pradel. 2005. U-CARE 2.2 User's Manual. Centre for, UMR 5175, CNRS, Monpellier, France.

Conn, P. B., W. L. Kendall, and M. D. Samuel. 2004. A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. Biometrics 60:900–909.

Daan, S., C. Deerenberg, and C. Dijkstra. 1996. Increased daily work precipitates natural death in the kestrel. Journal of Animal Ecology 65:539–544.

Dijkstra, C., A. Bult, S. Bijlsma, S. Daan, T. Meijer, and M. Zijlstra. 1990. Brood size manipulations in the kestrel *Falco tinnunculus*: effects on offspring and parent survival. Journal of Animal Ecology 59:269–286.

Estep, J. A. 1989. Biology, movements, and habitat relationships of the Swainson's hawk in the Central Valley of California. 1986–1987. Pages 52. California Department of Fish and Game, Nongame Bird, and Mammal Section Report, Sacramento, USA.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Department of Agriculture, Forest Service, Portland, Oregon, USA.

Goldstein, M. I., T. E. Lacher, Jr., B. Woodbridge, M. J. Bechard, S. B. Canavelli, M. E. Zaccagnini, G. P. Cobb, E. J. Scollon, R. Tribolet, and M. J. Hooper. 1999a. Monocrotophos-induced mass mortality of Swainson's hawks in Argentina, 1995–96. Ecotoxicology 8:201–214.

Goldstein, M. I., T. E. Lacher, Jr., M. E. Zaccagnini, M. L. Parker, and M. J. Hooper. 1999b. Monitoring and assessment of Swainson's hawks in Argentina following restrictions on monocrotophos use, 1996–97. Ecotoxicology 8:215–224.

Goldstein, M. I., B. Woodbridge, M. E. Zaccagnini, S. B. Canavelli, and A. Lanusse. 1996. An assessment of mortality of Swainson's hawks on wintering grounds in Argentina. Journal of Raptor Research 30:106–107.

Golet, G. H., D. B. Irons, and J. A. Estes. 1998. Survival costs of chick rearing in black-legged kittiwakes. Journal of Animal Ecology 67:827–841.

Heppell, S. S., C. Pfister, and H. de Kroon. 2000. Elasticity analysis in population biology: methods and applications. Ecology 81:605–606.

Herron, G. B., C. A. Mortimore, and M. S. Rawlings. 1985. Nevada raptors: their biology and management, Biological Bulletin. Nevada Department of Wildlife, Reno, USA.

Horak P., and J. D. Lebreton. 2008. Survival of adult great tits *Parus major* in relation to sex and habitat; a comparison of urban and rural populations. Ibis 140:205–209.

Houston, C. S. 2005. Swainson's hawk longevity, colour banding and natal dispersal. Blue Jay 63:31–39.

Janes, S. W. 1994. Partial loss of red-tailed hawk territories to Swainson's hawks: relations to habitat. Condor 96:52–57.

Littlefield, C. D., S. P. Thompson, and B. D. Ehlers. 1984. History and present status of Swainson's hawks in southeast Oregon. Journal of Raptor Research 18:1–5.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

McCleery, R. H., C. M. Perrins, B. C. Sheldon, and A. Charmantier. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. Proceedings of the Royal Society B: Biological Sciences 275:963–970.

Newton, I., P. Rothery, and I. Wyllie. 1997. Age-related survival in female sparrowhawks *Accipiter nisus*. Ibis 139:25–30.

Pianka, E. R. 1970. On r and K selection. American Naturalist 104:592–597.

Pilz W. R., and L. K. Seibert. 1978. Fratricide and cannibalism in Swainson's hawk. Auk 95:584–585.

Pradel, R., O. Gimenez, and J. Lebreton. 2005. Principles and interest of GOF tests for multistate capture-recapture models. Animal Biodiversity and Conservation 28:189–204.

Ricklefs, R. E. 2000. Intrinsic aging-related mortality in birds. Journal of Avian Biology 31:103–111.

Ricklefs R. E., and M. Wikelski. 2002. The physiology/life-history nexus. Trends in Ecology and Evolution 17:462–468.

Roff, D. 2002. Life history evolution. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Saether B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Schmutz, J. K., P. D. McLoughlin, and C. S. Houston. 2006. Demography of Swainson's hawks breeding in western Canada. Journal of Wildlife Management 70:1455–1460.

Stauss, M. J., J. F. Burkhardt, and J. Tomiuk. 2005. Foraging flight distances as a measure of parental effort in blue tits *Parus caeruleus* differ with environmental conditions. Journal of Avian Biology 36:47–56.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, England.

Swolgaard, C. A., K. A. Reeves, and D. A. Bell. 2008. Foraging by Swainson's hawks in a vineyard-dominated landscape. Journal of Raptor Research 42:188–196.

Whisson, D. A., S. B. Orloff, and D. L. Lancaster. 1999. Alfalfa yield loss from Belding's ground squirrels in northeastern California. Wildlife Society Bulletin 27:178–183.

Williams, P. D., T. Day, Q. Fletcher, and L. Rowe. 2006. The shaping of senescence in the wild. Trends in Ecology & Evolution 21:458–463.

With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152–3167.

Woodbridge, B. 1991. Habitat selection by nesting Swainson's hawk: a hierarchical approach. Thesis, Oregon State University, Corvallis, USA.

Woodbridge, B., K. K. Finley, and S. T. Seager. 1995. An investigation of the Swainson's hawk in Argentina. Journal of Raptor Research 29:202–204.

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