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Research Paper

High post-fledging survival and site persistence using mark-resight methodology for Oregon Vesper Sparrows in the Willamette Valley, Oregon

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ABSTRACT. The ecology of the post-fledging period for small passerine birds is one of the least known stages of the avian life cycle with high rates of mortality for many species. We examined post-fledging survival and site persistence of Oregon Vesper Sparrows (*Pooecetes gramineus affinis*) based on extensive temporal and spatial implementation of mark-resight methodology in western Oregon, 2017–2021. Our analyses focused on a comparison of descriptive apparent survival estimates (i.e., return rates) uncorrected for detectability and modeled apparent survival estimates corrected for detectability using Program MARK. Modeled survival estimates were only slightly higher than descriptive survival estimates at three weeks (0.754 and 0.689), six weeks (0.659 and 0.617), and nine weeks (0.629 and 0.561). Both estimates were lowest at three weeks post-fledging (0.754 and 0.689), and higher in weeks 3–6 (0.874 and 0.897), and weeks 6–9 (0.954 and 0.893). The best supported model included an effect of fledgling age in weeks on survival probability, and additive effects of site, effort, and week of season on detection probability. There was a live resight during the post-fledging period of at least one bird from 94.9% of the successfully fledged nests. Site persistence greater than 50 days was 0.838. Mean site persistence was 78.1 days and longest site persistence for an individual bird was 115 days. Our results suggest that an extensive mark-resight effort can address detectability concerns and provide an approximation of true post-fledging survival estimates. Our post-fledging survival estimates are the highest reported for a grassland bird, and yet they contrast with the expectations of the methodology and the literature on post-fledging survival of grassland birds, which is mostly derived from radio-tracking methodology. These results along with recent meta-analyses from other researchers raise concerns about unreported and unknown but expected mortality in grassland nestlings and fledglings from additive predation due to radio-tracking attachments and devices.

Taux élevé de survie et de persistance sur site mis en évidence par la méthodologie de marquage-relecture chez le Bruant vespéral de l'Oregon dans la vallée de la Willamette, en Oregon

RÉSUMÉ. L'écologie de la période qui suit l'envol des petits passereaux est l'une des étapes les moins connues du cycle de vie des oiseaux et le taux de mortalité est élevé pour de nombreuses espèces. Nous avons étudié le taux de survie et la persistance sur site après l'envol chez le Bruant vespéral de l'Oregon (*Pooecetes gramineus affinis*) en déployant la méthode de marquage-relecture sur une large échelle spatiotemporelle dans l'ouest de l'Oregon entre 2017 et 2021. Nos analyses se sont concentrées sur la comparaison des estimations descriptives de la survie apparente (assimilées à un taux de retour) non corrigée pour la détectabilité des individus et les estimations de la survie apparente modélisée avec correction selon la détectabilité en utilisant le programme MARK. Les estimations de survie modélisées n'étaient que légèrement supérieures aux estimations de survie descriptives trois semaines (0,754 vs 0,689), six semaines (0,659 vs 0,617) et neuf semaines (0,629 vs 0,561) après l'envol. Les deux estimations étaient les plus basses trois semaines après l'envol (0,754 et 0,689), et plus élevées pendant les semaines 3 à 6 (0,874 et 0,897), et les semaines 6 à 9 (0,954 et 0,893). Le modèle considéré comme le plus représentatif mettait en évidence l'effet de l'âge des oisillons (en nombre de semaines) sur la probabilité de survie, et des effets additionnels du site, de l'effort de prospection et de l'avancement dans la saison (indiqué en nombre de semaines) sur la probabilité de détection. Parmi les nids où un succès à l'envol a été constaté, au moins un juvénile a été revu au cours de la période suivant l'envol dans 94,9 % des cas. Le taux de persistance sur le site au-delà de 50 jours était de 0,838. En moyenne, ce taux s'élevait à 78,1 jours et la plus longue persistance sur le site pour un individu a atteint 115 jours. Nos résultats suggèrent qu'un effort important de marquage-relecture peut résoudre les problèmes de détectabilité et fournir une approximation des estimations des taux de survie réels après l'envol. Nos estimations des taux de survie après l'envol constituent les valeurs les plus élevées jamais rapportées dans le cas d'un oiseau des prairies, mais elles se distinguent nettement des prévisions attendues avec cette méthode et dans la littérature au sujet de la survie juvénile après l'envol des oiseaux des prairies, qui découlent principalement de la méthodologie de radiopistage. Ces résultats, ainsi que les méta-analyses récentes d'autres chercheurs, soulèvent des inquiétudes quant à une éventuelle mortalité non signalée, ou inconnue mais probable, des jeunes oiseaux des prairies, au nid ou juste après l'envol, du fait d'une prédation accrue due aux dispositifs de radiopistage et à leurs systèmes de fixation.

Key Words: *grassland birds; juvenile survival; mark-resight; mortality; post-fledging; Program MARK*

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INTRODUCTION

The post-fledging stage of the avian life cycle for a migratory bird is usually defined as the time between when a bird leaves its nest and when it disperses or migrates from its natal site (Cox et al. 2014, Naef-Daenzer and Grüebler 2016). The ecology of the post-fledging period for small passerine birds is an understudied stage, in large part because of the relative difficulty of studying it (Naef-Daenzer et al. 2001, Dybala et al. 2013). It is believed to be a critical stage in terms of a species population status because of the high rates of mortality for many species (Kershner et al. 2004, Anders and Marshall 2005, Naef-Daenzer and Grüebler 2016), and its influence on population growth and stability (Saether and Bakke 2000). It may also function as a survival bottleneck in the first year of a bird's life (Grüebler et al. 2014, Naef-Daenzer and Grüebler 2016).

The post-fledging period for grassland birds is characterized by a dependent period under care of the parents, and an independent period of self-sufficiency prior to migration (Young et al. 2019). The dependent period is usually 2–3 weeks long with limited fledgling mobility and high vulnerability to mortality from many factors but especially predation (Yackel Adams et al. 2001, Kershner et al. 2004, Davis and Fisher 2009). The independent period is characterized by developing flight skills and self-sufficiency, and energy-consuming needs for pre-formative molt and fat reserves for migration (Hovick et al. 2011).

Mark-resight methodology (McClintock and White 2009) to derive post-fledging survival estimates based on resighting of color-banded birds can be labor intensive because of the challenge of locating and identifying birds (Suedkamp Wells et al. 2007, Naef-Daenzer and Grüebler 2016), and ineffective because of the secretive behavior of fledglings, especially during the first 2–3 weeks after fledging (Anthony et al. 2013). Even after fledgling birds achieve independence, mark-resight results can be biased toward detection of short distance movements if effort is limited to a site or there are dispersal events that go beyond those boundaries (Baker et al. 1995, Craig et al. 2015). Thus, it has been widely recognized that any use of the mark-resight methodology must account for reduced detectability (Lebreton et al. 1992), and there is uncertainty about separating mortality from survival with emigration when birds are undetected (Cooper et al. 2008, Schmidt et al. 2008).

The development of radio-tracking technologies to accommodate small birds has resulted in less use of mark-resight methodology and expanded our knowledge of the ecology of the post-fledging period (Cox et al. 2014, Naef-Daenzer and Grüebler 2016). The most consistent pattern that has been documented for grassland birds is that mortality is highest during the first few days to one week post-fledging (Fisher and Davis 2011, Jones 2016, Bernath-Plaisted et al. 2021). As flight capabilities increase with age, mortality rates decrease and daily movements increase (Kershner et al. 2004, Davis and Fisher 2009, Small et al. 2015).

Despite advances in understanding the post-fledging period of grassland birds from the use of radio-tracking devices, few of the studies have lasted beyond 3–4 weeks (i.e., the approximate life of transmitters on the smaller birds) and cannot provide documentation of the occurrence or degree of dispersal to distances that would compromise survival estimates from mark-resight methodology. Among those that did extend multiple months to migration, Anthony et al. (2013) reported movements of only a couple hundred meters for Grasshopper Sparrow (*Ammodramus savannarum*), and Kershner et al. (2004) indicated high retention of Eastern Meadowlarks (*Sturnella magna*) on or near their natal grounds.

There have been multiple reports of no measurable negative effect of attachment of radio-tracking devices and harnesses on survival of nestling or fledgling grassland birds (Yackel Adams et al. 2006, Berkeley et al. 2007, Fisher and Davis 2011, Hovick et al. 2011). However, there have been some studies that have documented mortality directly related to the transmitter and harnesses (Yackel Adams et al. 2006, van Vliet and Stuchbury 2018, Young et al. 2019). Recent meta-analyses suggest even greater concern (Barron et al. 2010, Hill and Elphick 2011).

Oregon Vesper Sparrow (*Poocetes gramineus affinis*) is a subspecies of the wide-ranging Vesper Sparrow (Jones and Cornely 2002). Historically, it was a relatively common breeding bird throughout grassland and savannah habitats from southwestern British Columbia, through western Washington and Oregon, and into northwestern California (Altman 2011). Currently, its breeding range has contracted from British Columbia (COSEWIC 2018) and California (B. Altman and J. Geier, *personal observation*), and its wintering range from Baja (Patten et al. 2003) and southern California (Erickson 2008). Breeding Bird Survey data indicate a statistically significant declining population trend of 5.5%/year throughout their range (Sauer et al. 2017). It is considered of high conservation concern by all natural resource entities within its breeding and wintering range with a recent population estimate of approximately 3000 birds (Altman *unpublished data*). It was petitioned for listing under the U.S. Endangered Species Act (ESA) in November 2017, which resulted in a "may be warranted" finding in June 2018 (Federal Register 2018). The U.S. Fish and Wildlife Service (USFWS) is currently initiating a status review to determine if ESA listing is appropriate with a projected decision date in fall 2026 (USFWS 2024).

Herein, we report on post-fledging survival and site persistence of Oregon Vesper Sparrows based on use of the mark-resight methodology with color-banded birds from two sites in western Oregon as part of a demographic study on a larger metapopulation. Our objectives for this component of the project were to (1) assess survival during the post-fledging period to determine whether it is a limiting factor in population status, (2) assess persistence at the natal site during the post-fledging period to determine the efficacy of mark-resight methodology, and (3) compare our results with other post-fledging studies of grassland birds that used radio-tracking methodology.

METHODS

Study sites

Bald Hill Farm is an approximately 245-hectare property 3.2 kilometers west of Corvallis, Oregon, owned by Greenbelt Land Trust. It is in the foothills of the transition between the Willamette Valley and Coast Range Mountains ecoregions embedded within forest and developed lands and is managed for both conservation (i.e., prairie restoration) and working lands values (i.e., cattle grazing). The study was conducted on approximately 65 hectares of grazed pastureland and 25 hectares of prairie restoration that has supported a recent population of 13–20 pairs of Oregon Vesper Sparrows for at least the last 10 years.

Soap Creek Ranch is an approximately 730-hectare property 14.5 kilometers north of Corvallis, Oregon, owned by Oregon State University. It is in the foothills of the transition between the Willamette Valley and Coast Range Mountains ecoregions embedded within forest and agricultural lands and is managed by the Department of Animal and Rangeland Sciences for cattle forage and production, research, classes, student projects, and agricultural extension activities. The study was conducted on approximately 50 hectares of grazed pastureland that has supported a recent population of 19–24 pairs of Oregon Vesper Sparrows.

Both sites are dominated by non-native grasses and forbs except for the prairie at Bald Hill Farm, which has been seeded to native grasses and forbs (e.g., *Festuca roemeri*, *Prunella vulgaris*, *Sidalcia virgata*) with varying degrees of success. Dominant species in the pastureland at Bald Hill Farm are three forbs, *Daucus carota*, *Madia gracilis*, and *Plantago lanceolata*, and one grass, *Agrostis capillaris*. Dominant species at Soap Creek Ranch are three grasses, *Bromus hordeaceus*, *Hordeum jubatum*, and *Lolium perenne*, and one forb, *Daucus carota*. Scattered trees (e.g., *Quercus garryana*) and shrubs (e.g., *Crataegus monogyna*, *Rubus armeniacus*) are present at both sites (< 10% cover).

The two properties are approximately 13 kilometers apart. There were four other sites visited regularly with similar-sized populations of Oregon Vesper Sparrow within an approximately 24-kilometer radius of Corvallis, and 6–10 additional sites with small populations or suitable habitat visited occasionally as part of the larger metapopulation study. All the sites occur within a landscape of isolated patches of suitable habitat amid mostly unsuitable habitat in forests, agricultural fields, and the developed human landscape. The spatial distinctness of habitat and the degree of coverage provided opportunities to document dispersal events both during the post-fledging period and in the subsequent nesting season as first-year breeding birds.

Data collection

We collected data from 2017 to 2021 using the mark-resight method (McClintock and White 2009) for birds that had been color-banded as nestlings and successfully fledged. Nests were located using systematic and behavioral methods (Martin and Geupel 1993, Winter et al. 2003), and opportunistically when walking through an area and flushing a bird off a nest. The methods included rope-dragging (Winter et al. 2003, Giovanni et al. 2015) and observations of nesting behaviors (e.g., carrying nesting material or food, females returning to an area on multiple occasions, repeated alarm calls in an area).

Nest sites were georeferenced and marked by placing natural material (e.g., rocks, sticks) within a few meters of the nest in a manner conducive to relocation yet minimal in visual prominence. Nests were revisited in a manner to minimize predator attraction and investigator-induced predation including varying the direction and exit of approach to a nest, observations at a distance when possible, and use of sticks rather than hands for vegetation adjustment to see into the nest (Martin and Geupel 1993). Nests were checked every 2–3 days (1–2 days during expected hatching and fledging dates) until either the young fledged or the nest failed. A nest fledging at least one young was considered successful (Dinsmore et al. 2002). Nestlings were color-banded at 5–6 days old to avoid force-fledging closer to the typical 8–10 days at age of fledging. Each nestling was uniquely banded with a U.S. Geological Survey aluminum numbered band and color-band on the right leg and two color-bands on the left leg.

There were 1–3 individuals (same three people every year) resighting color-banded juveniles using spotting scopes every day in June and July while nest monitoring was occurring. During the post-breeding period, there were 1–2 individuals focusing on resights 4–6 days a week in August (Bald Hill Farm 2017–2018 and Soap Creek Ranch 2017), and 3–5 days a week in September (Bald Hill Farm 2019–2021 and Soap Creek Ranch 2018–2021) until migration typically in the last 10 days of September. Although daily effort was reduced in August and September, the sole focus was on resights unlike when nests were active, and the birds' flocking behavior at that time enhanced likelihood of detectability.

Statistical analyses

We calculated post-fledging survival from resighting data from the entire study period (i.e., 2017–2021). We present both descriptive apparent survival estimates without corrections for detection probability (i.e., return rates) and modeled apparent survival estimates using Program MARK (White and Burnham 1999). Neither method represents true survival estimates, as even models that account for detection probability cannot distinguish mortality from permanent emigration (although see Discussion: Mark-resight and true survival). We calculated survival for three post-fledging periods: at three weeks when birds reach independence and mortality rates level off (Young et al. 2019), at six weeks when survival rates are similar to adult birds (Cox et al. 2014), and at nine weeks to document survival well into the independent period and the approximate maximum amount of time a late fledgling (i.e., mid to late July) could spend at the natal site prior to migration in late September. We included dispersal events in the analyses of survival but not site persistence.

In our modeled survival analyses using Program MARK, we compiled observations of color-banded juveniles by week starting with the first week that nestlings fledged in any year (week starting on ordinal date 148) and continuing for up to the next 19 weeks. This resulted in a total of 20 encounter occasions encompassing 19 survival intervals: 18 weekly post-fledging survival intervals, and one 28-week overwinter survival interval. Overwinter survival was not a focus of this analysis, but we included this interval to better calculate post-fledging detection probabilities by accounting for several juveniles that were not observed later in the post-fledging period but survived and returned the following spring (e.g., 12 that were not observed after week 7, five that were not observed after week 4, etc.).

We modeled survival and detection probabilities using Cormack-Jolly-Seber (CJS) models in Program MARK (White and Burnham 1999). We used an information theoretic approach to model selection and interpreted results for models with the lowest Akaike's information criterion for small datasets (AICc; Burnham and Anderson 2002). We calculated the variance inflation factor ($\hat{c}$) via the median c-hat procedure in Program

Table 1. Presents QAICc values, differences between current QAICc and QAICc value for the best model (ΔQAICc), QAICc weights (w_i), model likelihood, and the number of theoretically estimable parameters (K) for each candidate model describing Oregon Vesper Sparrow (*Pooecetes gramineus affinis*) fledgling survival (φ) and detection probabilities (p). Variables in parentheses give parameterization for φ and p (see Methods for definitions). A median c-hat test on the most saturated model in the model set revealed a minor lack of fit to the data, so a $\hat{c}$ adjustment was used ($\hat{c}$ = 1.33).

Model	QAICc	ΔQAICc	w_i	Model Likelihood	K
φ(age), *p*(site+effort+week)	2034.18	0	0.547	1	40
φ(age+site), *p*(site+effort+week)	2036.23	2.05	0.196	0.359	41
φ(age+year), *p*(site+effort+week)	2036.38	2.20	0.182	0.333	44
φ(age+site+year), *p*(site+effort+week)	2038.54	4.36	0.062	0.113	45
φ(age), *p*(effort+week)	2041.67	7.50	0.013	0.024	39
φ(age), *p*(site*week+effort)	2057.81	23.64	0	0	58
φ(week), *p*(site+effort+week)	2061.93	27.75	0	0	40
φ(year), *p*(site+effort+week)	2065.91	31.74	0	0	26
φ(site+year), *p*(site+effort+week)	2068.03	33.86	0	0	27
φ(age*site), *p*(site+effort+week)	2069.63	35.45	0	0	59
φ(site), *p*(site+effort+week)	2069.86	35.68	0	0	23
φ(age), *p*(site+week)	2087.43	53.25	0	0	39
φ(age), *p*(site*week)	2111.07	76.89	0	0	57
φ(age), *p*(week)	2120.71	86.53	0	0	38
φ(age+site), *p*(week)	2122.23	88.06	0	0	39
φ(week), *p*(week)	2148.90	114.73	0	0	38
φ(age*site), *p*(site*week)	2151.41	117.23	0	0	76
φ(site), *p*(week)	2167.25	133.07	0	0	21
φ(age), *p*(site+effort)	2287.30	253.13	0	0	22
φ(age), *p*(effort)	2292.04	257.86	0	0	21
φ(age), *p*(site)	2323.46	289.28	0	0	21
φ(week), *p*(site)	2363.20	329.03	0	0	21
φ(.), *p*(.) - null	2450.56	416.38	0	0	2
φ(age*week), *p*(site+effort+week)	2469.88	435.71	0	0	211
φ(age*week), *p*(week)	2548.33	514.16	0	0	209
φ(age*week), *p*(age*week)	3266.71	1232.53	0	0	380

MARK, and then used it to adjust AICc values through quasi-likelihood (QAICc) due to a minor departure from goodness of fit ($\hat{c}$ = 1.33; Burnham and Anderson 2002). We examined effects of site, year, fledgling age (a categorical effect of the number of weeks out of the nest, 0–18 weeks), and time (week of season, a categorical effect with week 1 starting on ordinal date 148, week 2 starting on date 155, etc.), as well as additive and interactive combinations of these variables on weekly post-fledging survival (Table 1). Sex was not examined because most individuals (72.5%) were of unknown sex (sex could only be determined in the bird's second year if it returned and exhibited sex-specific behaviors). We examined models with detection probabilities varying by time (week of season), site, resighting effort (number of total person-days spent resighting for a given site and season), and both additive and interactive combinations of these variables. The models were compared to a null model (i.e., one with constant survival and detection probabilities).

We calculated survival estimates from the most well-supported models in three progressive three-week periods (weeks 0–3, 3–6, and 6–9) by multiplying weekly estimates together, and also calculated survival estimates for three cumulative periods (weeks 0–3, 0–6, and 0–9). Standard errors and 95% confidence intervals of weekly survival probabilities were calculated in Program MARK, while those of survival parameters that are products of weekly parameters were calculated using the Delta method (Seber 1982, Powell 2007). We used the Adjusted Wald Method (Bonett and Price 2012) for calculating standard error and 95% confidence intervals of the descriptive survival estimates, which represent a proportion of survival from binomial data.

We calculated site persistence as the number of days from fledging to the last sighting on the natal site prior to migration. We assumed residence during the period from fledging to the last resight based on most juveniles having numerous resights between those dates and the low likelihood of departure and then return to the site. We used data from 2018–2021 at Soap Creek Ranch and 2020–2021 at Bald Hill Farm when resight effort was most consistent through the end of September. We also calculated site persistence from the first nesting only (fledged prior to June 15) to September 1 to highlight the length of site persistence for birds fledging early in the nesting season. Resights greater than 50 days from fledging (i.e., approximately one month after achieving independence) were considered high site persistence. We refer to birds during the dependent period (i.e., approximately 0–3 weeks) as fledglings, and those after that as juveniles.

We conducted a systematic literature review to provide opportunities for comparative assessments (Table 2). This included inquiries in Google Scholar using the key words of grassland birds, post-fledging survival, juvenile survival, and mark-resight. We filtered for North American studies and reviewed the literature cited sections of all relevant retrieved articles for additional published sources.

Table 2. Post-fledging survival estimates for North American grassland birds.

Species	Location	Years	Habitat	Descriptive Survival (%)	Age (days)	Modeled Survival (%)	Bird Size (grams)	Citation
Oregon Vesper Sparrow *Pooecetes gramineus affinis*	Western Oregon	2017–2021	Prairie and pasture	69 *n* = 196	21	75	26	This project
Eastern Meadowlark *Sturnella magna*	Southeastern Illinois	1999–2000	Prairie	67 *n* = 43	90	56–69	90	Kershner et al. (2004)
Oregon Vesper Sparrow	Western Oregon	2017–2021	Prairie and pasture	62 *n* = 196	42	66	26	This project
Oregon Vesper Sparrow	Western Oregon	2017–2021	Prairie and pasture	56 *n* = 196	63	63	26	This project
Streaked Horned Lark *Eremophila alpestris strigata*	Western Washington	2016–2018	Prairie	54 *n* = 48	32	77	31	Slater et al., *unpublished data*
Eastern Meadowlark	Southwestern Missouri	2002–2004	Grazed prairie	51 *n* = 164	72	63	90	Suedkamp Wells (2005) Suedkamp Wells et al. (2007)
Western Meadowlark *Sturnella neglecta*	Central Nebraska	2006–2007	Prairie	50 *n* = 46	28	59	97	Giovanni et al. (2015)
Dickcissel *Spiza americana*	Eastern Nebraska and western Iowa	2003–2004	Tallgrass prairie	39 *n* = 52	28		27	Berkeley et al. (2007)
Savannah Sparrow *Passerculus sandwichensis*	Southwestern Ontario	2016–2017	Non-agricultural grasslands	35 *n* = 34	21	27	20	van Vliet et al. (2020)
Dickcissel	Southwestern Missouri	2002–2004	Grazed prairie	34 *n* = 248	58	56	27	Suedkamp Wells (2005) Suedkamp Wells et al. (2007)
Dickcissel	Central Illinois	2014–2015	Grassland	33 *n* = 102	36	29	27	Jones (2016)
Dickcissel	Northwestern Mississippi	2006–2007	Row crop and grassland	32 *n* = 200	15		27	Conover (2009)
Grasshopper Sparrow *Ammodramus savannarum*	Western North Dakota and eastern Montana	2016–2018	Grazed pastureland	29 *n* = 86	20	55	17	Bernath-Plaisted et al. (2019) Bernath-Plaisted et al. (2021)
Grasshopper Sparrow	Southern Iowa	2009	Grazed pastureland	27 *n* = 37	14	21	17	Hovick et al. (2011)
Sprague's Pipit *Anthus spragueii*	Southern Saskatchewan	2004–2008	Grassland and pastureland	27 *n* = 49	26	29	25	Fisher and Davis (2011)
Henslow's Sparrow *Centronyx henslowii*	Southwestern Missouri	2015–2016	Grazed tallgrass prairie	26 *n* = 46	14	35	13	Young et al. (2019)
Lark Bunting *Calamospiza melanocorys*	Northeastern Colorado	2001	Grazed short-grass prairie	21 *n* = 58	22	36	38	Yackel Adams et al. (2006)
Savannah Sparrow	Southwestern Ontario	2016–2017	Agricultural grasslands	21 *n* = 14	21	17	20	van Vliet et al. (2020)
Baird's Sparrow *Centronyx bairdii*	Western North Dakota and eastern Montana	2016–2018	Grazed pastureland	18 *n* = 133	20	25	17.5	Bernath-Plaisted et al. (2019) Bernath-Plaisted et al. (2021)
Lark Bunting	Northeastern Colorado	2002	Grazed short-grass prairie	18 *n* = 82	22	28	38	Yackel Adams et al. (2006)

Studies are listed from the highest descriptive survival estimate to the lowest. Descriptive survival estimates are the number of birds radio-tagged as nestlings and tracked to a survival outcome during the study-specific post-fledgling period (i.e., age [minimum 14 days])/number of birds radio-tagged and fledged from successful nests. Descriptive survival estimates for Oregon Vesper Sparrow in this project are the number of birds color-banded as nestlings and resighted during the post-fledging period/number of birds color-banded and fledged from successful nests. Percents are rounded to the nearest whole number. *n* = sample size of total number of marked birds. Modeled survival estimates use modeling programs that account for detection probability (e.g., Program MARK). Size of birds from Sibley (2010). Note: not included here because of the short study period (i.e., nine days) is a descriptive survival estimate for Grasshopper Sparrow in Maryland of 83% (n = 15; Small et al. 2015).

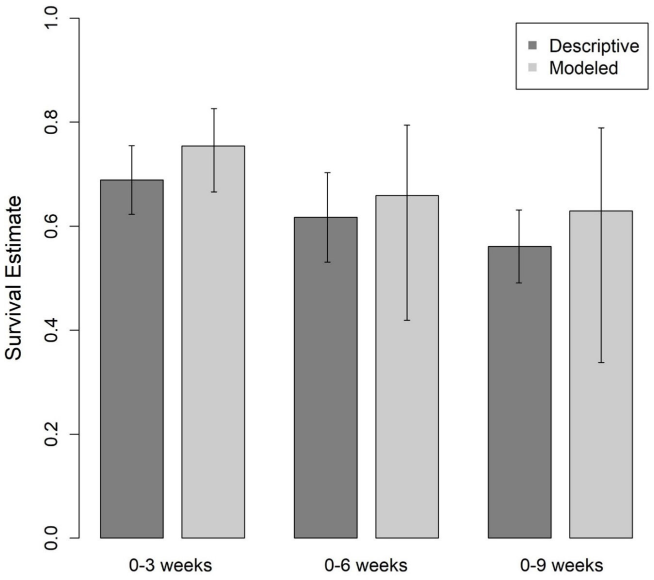
RESULTS

We color-banded 196 nestlings that successfully fledged from 74 nests at the two sites from 2017 to 2021. Sample sizes by year were: 2017 *n* = 25, 2018 *n* = 33, 2019 *n* = 34, 2020 *n* = 45, and 2021 *n* = 59. The earliest resight was on day 11 post-fledging. There was a resight during the post-fledging period of at least one bird from 94.9% of the successfully fledged nests. Among 79 color-banded nestlings that were resighted as first-year breeding adults, only four (5.1%) were not resighted during the post-fledging period.

Survival

Descriptive survival estimates were slightly lower than modeled survival estimates for all three cumulative (Fig. 1) and progressive (Table 3) time intervals except weeks 3–6 for the progressive analysis. Cumulative descriptive survival estimates across both sites were 0.689 (95% CI: 0.623–0.755) at three weeks, 0.617 (95% CI: 0.531–0.703) at six weeks, and 0.561 (95% CI: 0.491–0.631) at nine weeks (*n* = 196; Fig. 1). Modeled survival estimates were 0.754 (95% CI: 0.666–0.826) at three weeks, 0.659 (95% CI: 0.419–0.794) at six weeks, and 0.629 (95% CI: 0.338–0.789) at nine weeks (*n* = 196). Progressive descriptive survival estimates were lowest at three weeks post-fledging and mostly similar in weeks 3–6 and 6–9 (Table 3). Modeled survival estimates were also lowest at three weeks post-fledging but progressively higher in weeks 3–6 and 6–9 (Table 3). Bald Hill Farm had slightly lower progressive descriptive and modeled survival estimates than Soap Creek Ranch, but slightly higher modeled survival estimates. The annual

Fig. 1. Post-fledging descriptive and modeled apparent survival estimates and 95% confidence intervals at three cumulative time periods (0–3, 0–6, and 0–9 weeks) for Oregon Vesper Sparrows (*Pooecetes gramineus affinis*) at Bald Hill Farm and Soap Creek Ranch in western Oregon, 2017–2021.



range of descriptive survival estimates at six weeks were 47.1% (n = 34) to 75.0 % (n = 26) at Soap Creek Ranch, and 52.0% (n = 25) to 78.3% (n = 23) at Bald Hill Farm.

In the MARK analysis, the top three models comprised 92.5% of the model weight (Table 1). All models tested outranked the null model except for the most saturated models (those with an effect of age*week on survival). The highest-ranked model included an effect of fledgling age (in weeks) on survival, and additive effects of site, effort, and week of season on detection probability (φ = age, p = site + effort + week; Table 1). The next two best-supported models, including additive effects of age + site and age + year on weekly survival, had ΔQAICc scores < 2.3, near the commonly used threshold for substantial empirical support (Burnham and Anderson 2002). However, site (β estimate on the logit scale = -0.097; 95% CI = -0.56–0.37) and year (2017: β = 0.38, 95% CI = -0.39–1.14; 2018: β = 0.67, 95% CI = -0.34–1.37; 2019: β = 0.81, 95% CI = 0.90–1.53; 2020: β = 0.47, 95% CI = -0.14–1.08) can be considered uninformative as described by Arnold (2010) and are present in highly ranked models because the penalty for adding parameters does not outweigh the relatively strong explanatory power of fledgling age. Models of survival with site, year, or site + year but without an age effect have essentially no empirical support in the data (Table 1). Thus, we derived survival estimates pooled across sites from the top model alone, and survival estimates by site using the second-ranked model alone. Although site is an uninformative parameter, modeled survival estimates are presented by site to facilitate comparison to descriptive survival estimates (Table 3).

All candidate models with any appreciable support in the data (ΔQAICc < 7) included a categorical effect of week of season, site (β = -0.438; 95% CI: -0.717 – -0.160), and a numerical effect of effort (β = 0.045; 95% CI: 0.032–0.058) on detection probabilities (p). Detection probabilities were higher at Bald Hill Farm, but mean effort was lower, so these two effects somewhat ameliorated each other. Detection probabilities were low in the first week of the fledging season (when not many nests had fledged yet, and fledglings would be a maximum of one week old); the mean across sites was about 0.05. They were higher in the second week of the season (p = 0.14), and then remained higher in weeks 4–15 (mean p = 0.34, range: 0.25 to 0.53). By weeks 16 (p = 0.14) and 17 (p = 0.02), detection probabilities started dropping off sharply, and essentially reached zero in week 18, when most individuals had dispersed away from the study sites or initiated fall migration.

Site persistence

Mean site persistence was 78.1 days, including 70.4 days (n = 37) for Bald Hill Farm and 82.4 days (n = 68) for Soap Creek Ranch (Fig. 2). Site persistence greater than 50 days was 83.8% (n = 105). The longest site persistence for an individual bird was 115 days. Among juveniles that fledged prior to June 15 (i.e., first nesting) and survived through six weeks, 58.9% (n = 43) were present at the natal site at least to 1 September. In 2019 at Soap Creek Ranch, all 15 of the juveniles resighted at least once were detected on site at least 63 days after fledging, and six of those were still on the natal site at 100 days post-fledging.

Among the 196 nestlings that were color-banded and fledged successfully, there were six individuals with post-fledging dispersal events prior to migration (3.1%). This included examples of short distances (approximately three kilometers), longer distances (approximately 14 kilometers), both males and females (as determined by returns in the following year), multiple directions including south to north, and two examples of both directions between our two study sites.

DISCUSSION

Our results on post-fledging survival, acquired through mark-resight methodology, are the highest known for a grassland bird based on our literature review of approximately 15 studies, across nine states and two provinces, and among 10 species, all of which used radio-tracking methodology. They are also among the highest reported for any passerine bird (Cox et al. 2014). These results not only support the value of mark-resight methodology and our effort, but they also suggest the potential for methodological factors affecting the differences in post-fledging survival estimates from the radio-tracking studies.

Our modeled survival estimates, which adjust to account for imperfect detection, were only slightly higher than the descriptive survival estimates, indicating that mark-resight methodology and our degree of effort resulted in a high probability of detection of juvenile birds during the post-fledging period. Site persistence, a rarely reported metric and not available from the short-lived battery life of radio-tracking devices on small passerines, was also high throughout the entire 2–4 month post-fledging period prior to migration.

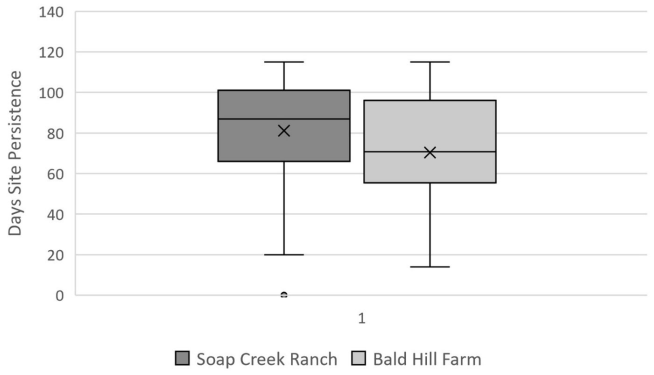
Survival

Prior to this study, there was no data on post-fledging survival of Oregon Vesper Sparrow or Vesper Sparrow (Jones and Cornely 2002). The descriptive and modeled apparent survival estimates at three weeks are more than twice as high as five of the six other studies among four different grassland bird species at that same

Table 3. Descriptive and modeled post-fledging apparent survival estimates (SE) during progressive three-week intervals (0–3, 3–6, 6–9 weeks) for Oregon Vesper Sparrows (*Poocetes gramineus affinis*) at Bald Hill Farm (*n* = 78) and Soap Creek Ranch (*n* = 118) in western Oregon, 2017–2021.

	Sites Pooled		Bald Hill Farm		Soap Creek Ranch	
Weeks	Descriptive	Modeled	Descriptive	Modeled	Descriptive	Modeled
0–3	0.689 (0.033)	0.754 (0.041)	0.680 (0.052)	0.761 (0.043)	0.695 (0.042)	0.743 (0.050)
3–6	0.897 (0.027)	0.874 (0.070)	0.868 (0.048)	0.878 (0.069)	0.915 (0.036)	0.867 (0.075)
6–9	0.893 (0.027)	0.954 (0.034)	0.870 (0.054)	0.956 (0.035)	0.909 (0.028)	0.952 (0.038)

Fig. 2. Post-fledging site persistence of Oregon Vesper Sparrows (*Poocetes gramineus affinis*) at Bald Hill Farm and Soap Creek Ranch in western Oregon, 2018–2021. Line within box is median line and X is the mean. Median line to end of box is the upper and lower quartile ranges, and the whiskers extend to maximum and minimums. The dot is an outlier.



age (Table 2). Our estimates are also higher than the mean post-fledging survival estimate of 58% at day 20 for 17 mostly forest-associated passerine species (Cox et al. 2014). The range of annual survival estimates among the two sites (47–78%) was higher than the 40% post-fledging survival threshold theorized as necessary to maintain population viability in passerine birds given average winter survival rates (Cox et al. 2014).

There was high mortality during the first three weeks post-fledging that leveled off after the dependent fledgling period. This pattern has been regularly reported for most passerines (Cox et al. 2014) including grassland birds (Suedkamp-Wells et al. 2007, Fisher and Davis 2011, Jones 2016, Bernath-Plaisted et al. 2021). Our lower descriptive than modeled survival estimates are consistent with other studies of grassland birds, although not always (Table 2).

Extension of the resight effort into August and September covering the entire post-fledging period resulted in many first resights of juveniles during that period and higher survival estimates than if effort had ceased at approximately one month from fledging like most radio-tracking post-fledging studies. This degree of effort fills an approximately 1–3 month gap in most post-fledging studies of grassland birds after the end of battery life in most transmitters (approximately 3–4 weeks) until departure for migration. Marshall et al. (2004) indicated that there is a direct relationship between the spatial and temporal effort expended in mark-resight and the degree to which post-fledging resighting and dispersal is documented for accurate survival estimates. Knowledge of survival during this juvenile period is essential to separate it from the previous dependent fledgling period and the subsequent migration and winter periods for understanding comparative mortality rates in different stages of the life cycle and targeting appropriate conservation actions.

Site persistence

Prior to this study, there was no data on post-fledging site persistence of Oregon Vesper Sparrow or Vesper Sparrow (Jones and Cornely 2002), and limited information on grassland birds. Most post-fledging research on grassland birds has focused on the dependent stage (over half the studies in Table 2) using radio-transmitters that are short-lived (i.e., less than 4 weeks) because of constraints on bird size (Yackel Adams et al. 2006, Berkeley et al. 2007, Hovick et al. 2011). The only studies that included much of the independent stage were on larger grassland birds that can carry larger and longer-lasting transmitters such as Eastern Meadowlark (Kershner et al. 2004, Suedkamp-Wells et al. 2007), Dickcissel (*Spiza americana*; Suedkamp-Wells et al. 2007), Streaked Horned Lark (*Eremophila alpestris strigata*; Slater et al., *unpublished data*), and Western Meadowlark (*Sturnella neglecta*; Giovanni et al. 2015).

Results from the few examples of monitoring juvenile grassland birds well into the independent period indicate that most movements were within the range of reasonable mark-resight survey distances. Anthony et al. (2013) used mist-netting to document that most Grasshopper Sparrow juveniles remained within a couple hundred meters of their natal nests for the months before their molt in early autumn. The longest recorded site persistence was 97 days and that bird moved approximately 0.8 kilometers. Most Eastern Meadowlark juveniles moved less than 1.5 kilometers, with a few beyond five kilometers, during a 90-day study period (Kershner et al. 2004), and in another study only began dispersing 0.5 kilometers from nest sites during the fourth week post-fledging (Giovanni et al. 2015). Our results support the limited literature that suggests that dispersal frequency or distance during the post-fledging period for some grassland birds has not been documented to the extent to be prohibitive for mark-resighting, and that some results suggest high retention of juveniles to the natal site for months prior to migration.

The need for juvenile Oregon Vesper Sparrows to undergo a preformative molt (Pyle 1997) is one factor that may have contributed to site persistence. This is also true for other grassland birds that undergo a partial or complete preformative molt that occurs at least partially if not completely on the natal site (Pyle

1997, Pyle et al. 2008). This requires substantial energy and resources during a sedentary period. Another factor that may have contributed to our high site persistence is the disjunct and patchy distribution of suitable habitat in the landscape. These conditions might discourage movement that requires traversing unsuitable habitat an unknown distance to locate suitable habitat, in comparison to large landscapes of suitable habitat (e.g., midwestern grasslands) where emigration can be incremental without any non-habitat barriers. The low rates of dispersal that we observed also would require that the vegetative habitat conditions at our study sites remain suitable throughout the post-fledging period, and that foraging resources are adequate for requirements of molt and development prior to migration. We did not attempt to evaluate this, but our high site persistence suggests these conditions were available.

True site persistence was likely higher, similar to results when correcting for detectability in the modeled survival estimates from Program MARK. The last resight of a juvenile would rarely be the day of departure from the site, especially when that resight is prior to mid-to-late September when migration departure has been documented via GPS-tagging (B. Altman, *unpublished data*). Further, there were two juveniles with less than 50 days of site persistence that returned the next year suggesting the potential for their undetected presence later than their last resight.

Our high site persistence suggests that nearly all juveniles surviving the first couple weeks spend 2–4 months prior to migration on the natal site. This has a direct bearing on the efficacy of mark-resight methodology for post-fledging survival estimates. The greater the site persistence, the greater the opportunity for resighting and the confidence in the methodology to detect juveniles and provide more accurate survival estimates while minimizing effort expended off-site.

Mark-resight and true survival

The use of mark-resight methodology to estimate post-fledging survival underestimates true survival because the methodology does not address all three components of an estimation of true survival: survival probability, emigration probability, and detection probability (Lebreton et al. 1992, Marshall et al. 2004, Anders and Marshall 2005). Even modeled survival estimates derived using CJS mark-resight models should still be considered minimum estimates because although they adjust survival estimates to account for imperfect detection, they cannot fully separate mortality from permanent emigration (Lebreton et al. 1992, Schaub and Royle 2014). However, we considered our apparent survival estimates based on mark-resight methodology to approximate true survival with minimal bias (Haas 1998, Martin et al. 2017) based on several factors related to detection and emigration probabilities.

Detection probability during the entire post-fledging period was likely high based on the live resight of at least one bird from 94.9% of nests that successfully fledged color-banded nestlings (n = 74). Additionally, only 5.1% (n = 4) of color-banded birds returning the following year were not resighted during the post-fledging period. If coverage had been insufficient and/or detectability was low, we would expect to see more first-year birds that had not been detected during the post-fledging period, especially with our high rate of returns.

Emigration probability was likely low based on several factors. There are a few inherent limitations on dispersal during the 2–4 month post-fledging period prior to migration including an approximately three week dependent period (Cox et al. 2014), the need for residency during a juvenile molt (Pyle 1997), and a period of residency prior to migration to accumulate resources. At both sites, movement from the nest can occur up to 1.3–1.6 kilometers but still be within the study site. Thus, our resight effort likely results in some within-site detections that would be considered emigration that is unaccounted for in other studies with smaller study site boundaries. Further, the resight coverage area outside the two study sites included many discrete sites within an approximately 24-kilometer distance in a highly fragmented landscape of suitable habitat patches with limited unsurveyed suitable habitat. We also documented six post-fledging dispersal events and an additional 40 adult dispersal events from all sites in the metapopulation indicating the ability of our effort and coverage to document dispersal when it occurred. All these factors support the comments of Marshall et al. (2004), Schaub et al. (2006), Lebreton et al. (2009), Cox and Jones (2010), and Schaub and Royle (2014) that as the resighting area becomes progressively larger and more emigrants are resighted, return rates begin to approximate true survival rates.

Last, our high post-fledging apparent survival estimates in conjunction with high apparent survival estimates for adult and first-year birds (approximately 62% and 34%, respectively), are collectively among the highest reported for a grassland bird, and for many migratory passerine bird species (Martin et al. 1995, Cox et al. 2014). It is unlikely that any substantial number of additional survivors went undetected, either within or outside the two sites, given that the minimum survival rate estimates based on apparent survival are already relatively high.

Mark-resight and radio-tracking

Our high post-fledging apparent survival estimates are counter to concerns about reduced detectability and low survival estimates with mark-resight methodology because of challenges in locating birds that are present and the uncertainty of mortality or emigration when birds are absent. Given these expectations, it seems likely that there should be many post-fledging survival estimates at least similar to if not greater than ours among the wide range of studies of grassland bird species and locations in Table 2. The consistent difference between those studies and this study is their use of radio-tracking methodology. Although individually there are likely other differences (e.g., predator communities, dispersal tendencies), collectively, the consistent use of radio-tracking and the degree of differences in survival estimates compared to our mark-resight methodology suggests that the differences may be a result of methodology rather than differences between species or populations.

Mark-resight methodology for post-fledging survival estimates has several disadvantages relative to radio-tracking. Radio-tracking can provide daily estimates of survival for the first approximately two weeks post-fledging when fledglings are mostly flightless, secretive, and unavailable for visual detection via mark-resighting. Radio-tracking allows for a much quicker location of the bird, more locations, consistency in tracking movements, and a definitive outcome of survival when located. It also ensures detectability of birds that are present and can provide some certainty between mortality and emigration if researchers extend the range of their search. Conversely, radio-tracking is temporally restrictive, whereas mark-resight is effective for the life of the bird not the life of the equipment.

The aforementioned data advantages of radio-tracking are well-documented, and its dominant use in post-fledging research on grassland birds reflects these advantages. However, this must be weighed with the reported and unreported negative impacts associated with the attachment of radio-tracking harnesses and devices, including mortality. Two recent meta-analyses summarized and elucidated those concerns. Barron et al. (2010) reviewed published papers that documented small but significant negative effects among adults for nest success and survival. They also concluded that it is probable that transmitters reduce fledgling survival creating a negative bias in the data.

Hill and Elphick (2011) conducted a survey among researchers and reported on the degree to which negative effects from radio-tracking attachments and devices occur that are not reported in the literature. Only two of the 60 respondents to the survey reported negative effects in peer-reviewed literature relative to actual occurrences, including mortality. They indicated that grassland birds were most susceptible to entanglement injuries and mortalities, especially recent fledglings that need to seek out dense vegetative cover to hide from predators (Kershner et al. 2004, Berkeley et al. 2007, Jones et al. 2017), resulting in constant contact between the antenna and harness with surrounding ground vegetation. This susceptibility is exacerbated based on stronger predation pressure than shrub or cavity-nesting passerines, which results in leaving the nest less-developed with a longer post-fledging flightless period and greater vulnerability to predation (Cheng and Martin 2012).

Entanglement from radio-tracking attachments leading to death of fledgling grassland birds has been reported for Henslow's Sparrow (*Centronyx henslowii*; Young et al. 2019), Savannah Sparrow (*Passerculus sandwichensis*; van Vliet and Stuchbury 2018), and Lark Bunting (*Calamospiza melanocorys*; Yackel Adams et al. 2006). Additionally, some entanglement events have resulted in escape assisted by researchers during tracking (Conover 2009, van Vliet and Stuchbury 2018). Other examples of mortality to nestling or fledgling grassland birds associated with radio-tracking attachments include mortality from transmitter wear or attachment glue (Hill and Elphick 2011), parental abandonment (Hill and Elphick 2011), and parental attempts to remove the attachments from nestlings (Mattsson et al. 2006).

Another consequence of radio-tracking on grassland bird fledglings is the potential for negative impacts associated with the frequency and duration of researcher checks on birds. For example, Berkeley et al. (2007) indicates when getting within 10 meters of the bird they allowed up to 30 minutes to locate the bird to assess survival. This regular intrusion has risks of stress and repeated flushing of birds, which would have energetic costs and increase the risk of mortality if predators are in the area. The researchers extended presence and vegetation trampling also could benefit predator attraction and exposure of fledglings. The effort required to determine the birds' status has also been reported to result in mortality due to accidental trampling of fledgling grassland birds (Young et al. 2019; Slater et al., *unpublished data*), which are especially vulnerable during the first week when they are relatively immobile and tend to remain motionless when approached. Conversely, mark-resight methodology is done at a distance and mostly during the independent juvenile period.

The low incidence of negative effects and mortality from radio-tracking fledgling grassland birds as reported in the literature is likely underestimating the issue based on the unreported occurrences (Hill and Elphick 2011). This is further exacerbated by some degree of unknown but expected and additive mortality resulting from predation that would otherwise not occur but is potentially enhanced by increased exposure and vulnerability to predators as the bird struggles with removal of equipment or extrication from entanglement. Although the frequency of those types of predation events beyond the expected baseline predation rate is unknown, it may be an important factor in the degree of difference between our post-fledging survival estimates using mark-resight methodology and those reported by others using radio-tracking technology.

CONCLUSIONS

Our high post-fledging apparent survival estimates along with high adult and first-year apparent survival estimates suggest that other factors may be limiting this metapopulation. These results provide critical data on parameters considered among the most difficult to obtain in a full-life cycle assessment for conservation status (i.e., post-fledging survival and site persistence) for a bird that has documented population declines and is being reviewed for listing under the ESA.

This project also provides an important example of how mark-resight methodology can address detectability concerns and provide an approximation of true post-fledging survival estimates. Our results and the results of others (e.g., Mattsson et al. 2006, Rush and Stutchbury 2008, Tarof et al. 2011, Vormwald et al. 2011) suggests that mark-resight methodology is a non-invasive alternative that can provide robust post-fledging survival estimates and other important metrics with comparatively no compromises to the safety and health of the birds compared to the alternative (e.g., radio-tracking of recently fledged young). This is especially important for endangered, threatened, or species of high conservation concern, such as Oregon Vesper Sparrow. If financial costs or convenience are prioritized over less invasive methodologies like mark-resight rather than radio-tracking for post-fledging studies of grassland birds, some birds and populations will be unnecessarily put at risk and the data may be biased. This will compromise conservation efforts and scientific integrity and responsibility.

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