Survival of juvenile Florida Scrub-Jays is habitat specific, positively correlated with month and negatively correlated with male breeder death

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Data availability: Analyses described herein can be reproduced using R script and data found attached.

ABSTRACT

Juvenile survival in birds is difficult to estimate but this vital rate can be an important consideration for management decisions. We estimated juvenile survival of cooperatively breeding Florida Scrub-Jays in a landscape degraded by fire suppression and fragmentation using data from marked (n=325), and unmarked juveniles (n=1306) with an integrated hierarchical Bayesian model. To assess the combined analysis we also analyzed these datasets separately with a Cormack-Jolly-Seber model (marked) and unmarked young model (unmarked). Our data consisted of monthly censuses of territorial family groups from Florida Scrub-Jay (Scrub-Jay) populations in East Central Florida collected over a 22 year period. Juvenile survival was estimated from July when young Scrub-Jays begin developing independence to March when they become first year individuals and grouped according to the habitat quality class of their natal territory that were based on shrub height (with intermediate shrub heights being optimal and short and tall shrub heights being suboptimal) and the presence of sandy openings (the preferred open having many sandy openings; closed not having enough). Parameter estimates in the combined analysis were intermediate to the separate analyses. Notable differences among in the separate analyses were that suboptimal habitat survival was lower in the unmarked analysis, the unmarked analysis showed a linear effect of time not seen in the marked analysis and there was an effect of male breeder death in the marked but not unmarked analysis. The combined data analysis provided more inference than did either data set analyzed separately including: juveniles in optimal-closed territories unexpectedly had higher survival than those in optimal-open, survival increased through time and male breeder death had a negative effect on survival. This study suggests that optimal-closed habitat may play an important role in juvenile Scrub-jay survival perhaps by providing better cover from predators and warrants further investigation for management implications.

Keywords: Aphelocoma coerulescens; cooperative breeder; Florida Scrub-Jay; habitat specific survival; hierarchical Bayesian model; juvenile survival; integrated model

LAY SUMMARY

- Habitat management is an important tool for species conservation in degraded habitat especially when habitat quality is transitional (i.e., varies with disturbance and succession) and where high-quality habitat is an exporter of individuals to low quality habitat (i.e., source sink dynamics).
- Considering how management actions affect all life-stages is important. Survival of juvenile birds can be difficult to estimate because of dispersal or migration but may be needed for proper species management. Non-migratory species offer a unique opportunity to include juvenile survival estimates into management plans.
- We estimated survival based on resighting marked and unmarked juvenile Florida Scrub-Jays (*Aphelocoma coerulescens*) using an integrated hierarchical Bayesian model. By also analyzing each data set separately we show the strength of using a combined model to make inference.
- We investigated survival in three habitat classes related to shrub height and the amount of open sandy patches that vary according to fire and subsequent shrub regrowth. Juvenile survival was highest in territories with medium height shrubs and few sandy openings. This result is unexpected and may have management implications.
- Survival increased across the post fledgling period possibly indicating that juvenile Scrub-Jays learn predator avoidance. Survival was negatively affected by male breeder death demonstrating the importance of family stability and possibly the number of siblings because larger groups of naïve juveniles attract predators.

INTRODUCTION

For species of conservation concern, understanding the relationship between habitat quality and population vital rates should be a priority (Marzluff et al. 2000). This is especially true for species that occupy transitional habitat that varies in quality temporally with succession and disturbance (Eaton et al. 2021) and where source sink dynamics apply (Pulliam 1988). Habitat-population relationships may vary among life-stages (Young et al. 2019), and juvenile survival can be an important driver of population growth in species exhibiting source sink dynamics (Donovan and Thompson III 2001). Cox (2014) found that most studies of post-fledgling survival found a direct relationship with habitat. A complete understanding of population vital rates and the factors that influence these rates is necessary to determine where in the life cycle population limitation occurs. This allows management decisions to focus on the life stage with the most impact on demographic performance (Anders and Marshall 2005, Drummond et al. 2019).

Philopatric, permanent resident species offer a special opportunity to estimate survival throughout the annual cycle (including juveniles) allowing investigation of the local factors that influence survival and possibly inform management to maximize first-year survival (Doherty Jr. and Grubb Jr 2002, Cox et al. 2014) or help managers assess habitat quality (Knutson et al. 2006, Arlt et al. 2008). The Florida Scrub-Jay (*Aphelocoma coerulescens*) is a good candidate species for the study of juvenile survival because Scrub-Jays maintain year round territories and are a cooperative breeding species where the young typically stay with the family unit beyond the natal year (i.e., the first year of life, Woolfenden and Fitzpatrick 1984), offering a rare opportunity to study this stage of life in an avian species. Sensitivity analyses have shown that

Scrub-Jay population trajectories are moderately sensitive to juvenile survival rates when compared to other demographic rates (Breininger 1999, Lacy and Breininger 2021).

Scrub-Jays occupy a mid-successional community of shrubs, sometimes with a sparse pine (*Pinus* species) overstory. Optimal habitat forms a low and open landscape with sandy gaps dispersed among the shrubs (oak scrub;Woolfenden and Fitzpatrick 1996, Schmalzer et al. 1999). The natural fire regime creates optimal habitat conditions with a mosaic of shrub heights between 1.2 -1.7 meters, and abundant sandy openings (Woolfenden and Fitzpatrick 1984, 1991, Breininger and Carter 2003, Breininger et al. 2014) favored by Scrub-jays (Fitzpatrick et al. 2016). Thus, territory quality is primarily determined by fire disturbance that alters shrub heights and the abundance of sandy openings. Fire kills above ground biomass, but shrubs resprout from underground rhizomes, succession resumes, and shrubs grow back to optimal height and then beyond (Schmalzer 2003, Fitzpatrick et al. 2016).

In our study population, fire suppression beginning in the 1950's (Larson 1952) altered the natural fire regime and degraded most Scrub-Jay territories via succession to suboptimal tall shrub heights and few openings (Breininger 1999, Duncan et al. 1999); Fire suppression continued until 1981 when land managers began to use prescribed fire to decrease hazardous fuel accumulations and later as a tool for scrub habitat management (Duncan et al. 1999). This fire suppression period and the ensuing fuel management and habitat restoration efforts created the current mosaic of habitat quality leading to source-sink dynamics within territory clusters (Breininger and Carter 2003). Recently burned territories with short regenerating shrubs and long unburned territories with overgrown tall shrubs have suboptimal vegetation height and are usually demographic sinks. Territories with intermediate height shrubs have optimal vegetation height and more often sources. Restoring long-lasting sandy openings (a key characteristic of high quality habitat) has proven difficult as openings that result from prescribed fire generally disappear as shrubs transition through the optimal height stage (Schmalzer and Hinkle 1992). Consequently, at the territory scale two classes of habitat quality occur within optimal height scrub due to fire mosaics within the territory (i.e., the extent of sandy openings). These classes differ in demographic performance (yearlings produced per pair-year). Territories with at least 10 percent of shrubs at optimal height amongst shorter shrubs and no more than an acre of taller shrubs together with 10-50% ground cover as sandy openings (optimal-open) outperform optimal height territories without openings (optimal-closed, Breininger et al. 2014, Lacy and Breininger 2021, Breininger et al. 2023). Thus, three classes of habitat quality occurred in the study populations: optimal-open (source) outperforms optimal-closed (intermediate) which outperforms suboptimal (sink). Optimal-closed territories do not contribute a net gain to population growth but act as a buffer for surplus breeding pairs (i.e., when no optimal-open habitat is available) and thus help support a larger population.

We sought to assess the degree to which juvenile survival estimates corresponded with the previously defined habitat quality classes because of the evidence of source sink dynamics in our population (Breininger and Carter 2003) and the moderate sensitivity of population growth to juvenile production. We expected optimal-open territories to have the highest juvenile survival rates similar to Fitzpatrick et al.'s (2016) "early postfire period" habitat followed by optimal-closed and suboptimal. We sought to determine how survival was affected by sociobiological factors that may be important to juvenile survival because juveniles are reliant on their family group for vigilance (Woolfenden and Fitzpatrick 1984, Hailman et al. 1994, Woolfenden and Fitzpatrick 1996) and older sibling (helpers) increase yearling production not only through contributions to provisioning of dependent young, but also territorial defense and predator vigilance (Woolfenden and Fitzpatrick 1984, Mumme 1992, Woolfenden and Fitzpatrick 1996). Also, our study population is located on Florida's Atlantic coast and is a major route and wintering grounds for migrating hawks (*Accipiter* spp.) and falconids (*Falco* spp.) that are known predators of adult and juvenile Scrub-Jays. This influx of predators during young Scrub-Jays' transition to first year individuals may play an important role in survival rates. This seasonal feature of the predator regime encountered by our study population (Breininger et al. 1996) may be important because varying extrinsic factors among populations, such as predation, can alter intrinsic population vital rates such as survival and recruitment (Newton 1998).

Thus, for each juvenile we quantified the number of helpers (helper count), juvenile siblings (sibling count) in the family and the number of juveniles in the territory cluster (cohort count). We predicted helper count would positively affect juvenile survival in our study population by augmenting family vigilance. We predicted that sibling count would negatively affect juvenile survival because larger numbers of naïve individuals would potentially attract more predators (Cresswell and Quinn 2011). Similarly, yet on a larger scale, we thought that cohort count might have a similar negative effect because jay territories are typically contiguous in the landscape forming neighborhoods of Scrub-Jay families (Woolfenden and Fitzpatrick 1984). We also quantified male and female breeder death (male death and female death) and predicted that male death and female death would negatively affect juvenile survival and further that male death would be more significant because this often leads to greater disruption of the family unit and territory integrity. Finally, we sought to confirm temporal effects on survival during the juvenile period. Siberian jays (*Perisoreus infaustus*) show an increase in survival after exposure to predator mobbing by family members (Griesser and Suzuki 2017). In a consistent fashion and also in agreement with Woolfenden and Fitzpatrick (1984) we expected juvenile Scrub-Jay survival would increase as foraging efficiency and vigilance improved.

Our primary objectives were to: 1) estimate survival of juvenile Scrub-Jays for each of the three territory quality classes described above, 2) determine the relative strength of sociobiological covariates potentially important to juvenile survival as well as temporal effects and 3) develop an integrated hierarchical Bayesian model to combine marked and unmarked data within a single analysis. We used a combined model because we had two datasets, a result of varying level of effort in study sites over a large geographic area and changing objectives during a long-term study and we thought each dataset could potentially provide valuable inference. To assess the combined model, we also separately modeled the marked data with a Cormack-Jolly-Seber model and the unmarked data with a dependent young survival model and compared the estimates of survival and detection as well as covariate signals of the three models,

METHODS

Data Description

Habitat quality within territories was classified annually by overlaying territory maps on digital ortho-rectified aerial photography. Visual classification specified textures that corresponded to vegetation height (see Breininger and Carter 2003); we binned territories into the defined habitat classifications. Sociobiological covariates for each territory were quantified from annual demographic data. Helper count was taken in March (at beginning of breeding season), sibling count and cohort count were taken in July (at beginning of capture history). Male death and female death that occurred between March and the following July and was coded as binary (1=death during year).

Two types of survival data were utilized. In the first type (hereafter the marked dataset) all nestlings were banded eleven days after hatching using a numbered metal leg band and a unique combination of color bands allowing identification of individuals. The marked dataset was collected from 1988 to 2009 as part of a long-term demographic monitoring effort of the Scrub-Jay population occurring on Merritt Island National Wildlife Refuge/John F. Kennedy Space Center (MINWR/KSC). During this period the populations under study were intensively monitored and we attempted to locate all nesting attempts before the penultimate egg was laid and thus clutch size and age of nestlings were known (see Carter et al. 2011). Nests were visited weekly to determine status and count eggs or nestlings until failure or fledging. Thereafter we conducted a monthly census within each territory to record observations of banded birds. In the second data type (hereafter the unmarked dataset) young were not banded in the nest but a monthly census like that for the marked data set was conducted within each territory to observe the total number of unmarked young alive with the family group. The unmarked dataset was collected from 1988 to 2014 as part of a larger and less intensive monitoring effort (i.e., no nest monitoring) of the Scrub-Jay metapopulation in East Central Florida (see, Breininger et al. 1995) and on MINWR/KSC (Figure 1).

Monthly capture histories were recorded beginning in July and continued through the following March just prior to the next breeding season. This 9 month period encapsulates the phase when young Scrub-Jays are learning survival skills, obtaining adult plumage, overwintering, and approaching their first year as helpers, or much less commonly, as novice breeders. Detection probabilities for adult Scrub-Jays are high (Breininger et al. 2009), and the cooperative breeding nature of Scrub-Jay families facilitated resighting both marked and unmarked young Scrub-Jays.

The marked dataset consisted of 325 individuals in 190 families; the unmarked dataset consisted of 1306 individuals in 648 families. Most territories were suboptimal in both datasets. (54% marked, 53% unmarked). Mean helper count was < 1 for both datasets. Helper count ranged from 0-9 per family; fifty-three percent (*n*=447) did not have helpers and most families with helpers (56%) had only 1 (*n*=220); 109 families had 2 helpers, 39 had 3 helpers, and 17 families had 4 helpers. Six families had more than 4 helpers. Sibling count was 1 in 35% (*n*=293), 2 in 31% (n=257), 3 in 16% (*n*=132) and 4 in 6% (*n*=47) of families. Eleven families (1%) had 5 or more juveniles and 98 (12%) had none. Mean cohort count was 14.0 (unmarked) and 15.0 (marked) and ranged from 0 to 54. The male breeder died in 124 families (unmarked) and 37 (unmarked). and the female breeder died in 126 families. Most male death (*n*=94) and female death (*n*=78) occurred in suboptimal territories. Thirty-three families lost both breeders.

Analysis

(Williams et al. 2001) We used 2 types of capture histories to estimate survival at the family group level (juveniles in a given territory and year): monthly detection data for marked individuals, and monthly counts of unmarked individuals. We analyzed our marked and unmarked data combined and separately. In the combined method we used an integrated hierarchical Bayesian model with the sub-model for the survival parameter shared by the marked and unmarked data sets, and separate detection sub-models for each type of data (Figure 2). Bayesian models with shared parameters allow data collected at different scales or with different methods to be combined (Fletcher Jr. et al. 2019, Miller et al. 2019, Schaub and Kéry 2021page

62-65). We also conducted separate analyses for each data set using the CJS model for the marked data, and the dependent young model for the unmarked data. We compared the estimates of survival from the combined model and from each of the individual models to better understand the combined model and the strength of the information about the effects on survival contained in each data set.

In the combined model we used a Bayesian state-space implementation of the CJS mark-recapture model to model the likelihood of the marked data (Kéry and Schaub 2012). The process model consisted of a latent state variable (Z_{it}) that recorded if individual i was alive during time interval (month) t, conditioned on the first capture of the individual. The process model then determined if the individual survived based on parameter $\phi_{g,t}$ which was a shared parameter in the integrated model (see below); the index specifies the group in month t. The observation model used the observed monthly capture history data to model detection probability $p_{g,t}$, conditioned on the individual being alive ($Z_{i,t}=1$).

$$Y_{i,t}|Z_{i,t} = Bernoulli(Z_{i,t} \cdot p_{g,t})$$

$$Z_{i,t}|Z_{i,t-1} = Bernoulli(Z_{i,t-1} \cdot \phi_{g,t})$$

$$Z_{i=f_i} = 1;\ Z_{i<f_i} = 0$$

Where f_i is the time interval when the individual was first detected. The basic assumptions of the CJS model are that marks are not lost and are perfectly identified when observed, observations are effectively instantaneous, and there is no unmodeled heterogeneity in survival or detection (Kéry and Schaub 2012).

To model the likelihood of the unmarked data we used a Bayesian implementation of the Lukacs et al. (2004) dependent young survival model, modified to allow the initial brood size to be estimated as a partially observed variable. Although we did not use informative priors for brood size, our model could accommodate this if a suitable independent source of data were available. In the original Lukacs et al. (2004) dependent young survival model it is assumed that initial brood size is perfectly observed. We modified this to allow the initial brood size to be greater than was ever observed, to allow for cases when the entire initial brood was never observed. The process model consisted of a latent state variable ($Q_{g,t}$) that recorded the number of individuals alive in each territory g during each time interval t, conditioned on the initial brood size which was imperfectly observed. The process model then determines how many of the individuals survive based on parameter $\phi_{g,t}$ which was a shared parameter in the integrated model (i.e., $_{g,t}$, see below). The observation model used the observed number of young ($W_{g,t}$) to model how many individuals were observed in territory g during time interval t with detection probability p conditioned on the latent number alive ($Q_{i,t}$).

$$W_{g,t}|Q_{g,t} = Binomial(Q_{g,t}, p_{g,t})$$

$$Q_{g,t}|Q_{g,t-1} \sim Binomial(Q_{g,t}, \phi_{g,t})$$

$$Q_{g,1} \sim Categorical(Brood\ Probabilities)$$

$$Brood\ Probabilities \sim Dirichlet(Observed\ Brood\ Probabilities)$$

In the combined model, the likelihoods for the two data sets shared parameters for survival (φ) which was modeled with group by time level covariate effects. For survival we modeled the effects of habitat (3 levels), a quadratic time effect (month of sampling), and the five sociobiological covariates. We modeled the effects of only habitat (3 levels) on each of the separate detection parameters (for marked and unmarked data) because we believed a priori that detection should differ among habitats, and since detection was a nuisance parameter we chose not to use information in the data to model other effects. The covariates were included in linear predictors using a logit transformation as (Eq.1):

$$\text{logit}(\phi_{g,t}) = \beta_{intercept} + \beta_t\text{*time} + \beta_{t2}\text{*time}^2 + \beta_{optimal\ open}\text{*I(optimal-open)} + \beta_{optimal\ closed}\text{*I(optimal-closed)} + \beta_{male\ death}\text{*I(male death}_g\text{)} + \beta_{female\ death}\text{*I(female death}_g\text{)} + \beta\ \text{*helper count}_g + \beta_{\text{sibling count}}\text{*sibling count}_g + \beta_{\text{cohort count}}\text{* cohort count}_g + \text{Territory}_g \quad \text{(Eq. 1)}$$

$$\text{logit}(p_{g,t}) = \beta_{intercept} + \beta_{medium\ open}\text{*I(optimal-open)} + \beta_{medium\ closed}\text{*I(optimal-closed)} + \text{Territory}_g$$

where g = group (specific to territory and year), t = linear time interval starting with 0 (July was in the intercept), t^2 = squared time interval, I(.) is an indicator for levels of a categorical variable, and Territory was a territory within year level random effect with the standard deviations modeled independently for survival and each detection parameter for the marked and unmarked data. These random effects were included to minimize the effect of overdispersion.

Bayesian models were fit using Markov Chain Monte Carlo (MCMC) methods using program JAGS 4.3.0 (Plummer 2017) implemented in R (R Core Team 2020) with the package jagsUI (Kellner 2019) and visualized using R packages coda (Plummer et al. 2006), ggmcmc (Fernández-i-Marín 2016), and bayesplot (Gabry and Mahr 2021). For all model parameters, except for the standard deviations of the random effects, we used normal priors with mean = 0 and variance = 100, which were uninformative on the logit scale which is contained mostly between +/- 6. For the priors for standard deviations of the random effects we used weakly informative distributions by taking the right half of a normal distributions with mean 0 and variance = 2. This produced a distribution similar in shape to the Half-Cauchy distribution recommended by (Gelman 2006), but with a much shorter tail. To check the influence of the weakly informative priors, we re-ran the model with broader priors on all random effects SD parameters. The estimates for all parameters were unchanged (within the MCMC error) indicating that the choice of prior was not influencing the results. For each analysis, we ran 3 chains, initialized with different random stating values, discarding at least the first 10,000 iterations as burn-in, then running additional samples until the Gelman-Rubin convergence diagnostic (R-hat) was less than 1.01, and the number of effective samples was estimated to be greater than 4000, for all parameters except for the random effects standard deviations which tend to converge much more slowly (the smallest number of effective samples among all standard deviation parameters after convergence was 1687) . We did not thin the MCMC posteriors (Link and Eaton 2012). We assessed goodness-of-fit with a posterior predictive test using a version of the Bayesian *p*-value that compared the fit of the observed cumulative empirical survival curve to the equivalent fit of data simulated under the model with estimated parameters (Schmidt et al. 2010). We used plots of the fit statistics to choose among alternative random effects designed to correct for overdispersion in each data set due to sharing of territory and study site, and year which has been observed to be important in previous studies. We scaled all continuous and count covariates by subtracting the mean and dividing by 2 standard deviations (Gelman 2008); this puts the regression coefficients for numerical and categorical covariates on similar scales allowing comparison of effect sizes. See the data availability section in acknowledgements for data and details of implementing the integrated Bayesian hierarchical model in JAGS via R.

RESULTS

As expected, the parameter estimates from the model applied to the combined dataset (hereafter combined analysis) were intermediate between those of the models applied to the marked data set (marked analysis) or the unmarked dataset (unmarked analysis) (Figure 3). The closer resemblance of the combined and unmarked analysis was probably due to the larger size of the unmarked data. Significant results of the combined analysis include a positive linear effect of time on survival, a strong positive effect in optimal-closed habitat and to a lesser extent in optimal-open and a negative effect of male breeder death (Table 1, Figure 4). Sibling count had a weak (overlapped zero) negative effect on survival, while none of the other covariates influenced survival (Table 1, Figure 4).

A key difference between the marked and unmarked analyses was that survival in suboptimal habitat was estimated to be lower in the unmarked analysis (Figure 3). Survival estimates for optimal-open and optimal-closed agreed more closely among the marked and unmarked analyses but optimal-closed habitat had higher predicted survival than suboptimal habitat for both marked and unmarked analyses while only optimal-open habitat survival was higher than suboptimal habitat survival in the unmarked analysis (Figure 3). The effect of time on survival differed somewhat between the marked and unmarked analyses. The unmarked analysis suggested a linear increase in survival over the capture history that was not apparent in the marked analysis (Figure 3, Figure 5). The effect of habitat on detection differed between the marked and unmarked analyses for optimal-open and optimal closed habitat. For the marked analysis (Table 2) detection was high in all habitat groups (optimal-open p=0.97 (0.94, 0.98), optimal-closed p=0.96 (0.93, 0.98) and suboptimal p=0.98 (0.96, 0.99). For the unmarked analysis (Table3) detection was lower in all habitat groups (optimal-open p=0.97 (0.95, 0.98), optimal-closed p=0.87 (0.81, 0.92) and suboptimal p=0.93 (0.91, 0.95).

DISCUSSION

Our estimates of juvenile Florida Scrub-jay survival rates mostly agreed across the three (marked, unmarked, combined) analyses for optimal-open and optimal-closed habitat. However, the survival estimate for suboptimal habitat was much lower for the unmarked analysis. One possible explanation for the difference could be that juveniles in suboptimal territories in the unmarked dataset had high levels of unobserved temporary emigration (birds not present during a census).(Lukacs et al. 2004) The unmarked dataset contained many territories in fragmented habitat in which juveniles might make lengthier daily movements during extra-territorial forays and this movement could negatively bias apparent survival. The unmarked dataset, while large, had the limitation of not being able to detect individuals outside of their territory. Alternatively, the difference in survival might be real and thus warrants further investigation. Despite this difference, covariate signals largely agreed among the models suggesting inference regarding their effects was robust.

Habitat had the strongest effect (in all analyses) suggesting habitat structure is a key determinant of juvenile survival. Unexpectedly, optimal-closed territories had the highest survival possibly because optimal-closed provided greater cover from aerial predators; this result may have management implications. Age (time) had a positive effect in the unmarked and combined analyses which fit with our hypothesis that survival would increase with time as foraging efficiency and predator avoidance improves; the absence of a time effect in the marked data set was possibly because of the small sample size. Male death had a negative effect in all the models and significantly so in the marked and combined models fitting our hypothesis of the importance of family stability for young Scrub-Jays. The other hypothesized sociobiological effects were not significant in any of the models possibly because these relationships are more complex than our analysis accounted for. Helper count had no effect and was possibly confounded with territory size. Sibling count and cohort count were consistently negative for all models but the estimates overlapped zero. Female death had a positive effect overlapping zero in the combined model and in our assessment was spurious.

Like survival, detection intercepts were also different between the marked and unmarked datasets with marked detection higher than unmarked. We think this again reflects the weakness of the unmarked dataset in not being able to detect individuals outside of the natal territory. Combining two data sets (marked and unmarked) took advantage of the strengths in each. The marked dataset offered the opportunity to use better information at the level of individuals, while the unmarked dataset offered much larger sample sizes and study area extent. Combining these data sets allowed for more precise and less biased parameter estimates than could be obtained from either separately and provided inference not afforded individually (i.e., time and male breeder death).

The effect of habitat is not completely consistent with Breininger et al. (2014) who found that yearling production was highest in optimal-open territories, in part because juvenile production is highest in optimal-open (Breininger et al. 2023). The unexpected results of optimal-closed territories having the highest survival provide motivation for further investigation to better understand possible alternate management strategies for this declining species. Studies of other species have shown the importance of understanding juvenile survival in the context of habitat (e.g., Streby et al. 2016, Young et al. 2019). Predation can be especially high in suboptimal conditions (Woolfenden and Fitzpatrick 1984, Fitzpatrick et al. 2016) and varies among populations; Accipiter and falconid species are numerous along the coastal sites studied here (Breininger et al. 1996, Breininger et al. 2009). Since most of the study population occurred in suboptimal conditions, we focused our a priori hypotheses mainly on mechanisms that may operate because of predation pressure and possibly generate habitat specific survival rates in juvenile Scrub-Jays. It is possible that dense vegetation structure in optimal-closed territories offered more aerial predator escape cover for juveniles.

It is also possible that undetected emigration (that can bias survival estimate low) may help explain our results because Scrub-Jays sometimes disperse at a young age and join an unrelated group (staging disperser); the reasons vary with sex but staging Scrub-Jays disperse farther than "direct dispersers" (that immediately become breeders) and are usually from high quality habitat (Suh et al. 2022). This early and farther dispersal could have biased apparent survival estimates in optimal-open territories (high quality and with typically more helpers). Second, Scrub-Jays disperse further (total distance) in fragmented habitat (Breininger 1999, Fitzpatrick et al. 1999, Coulon et al. 2010). We did not include a measure of habitat fragmentation in our analysis, but it is possible this dispersal trait also could have contributed to biased survival estimates (because most remaining Scrub-Jay habitat is fragmented to some extent). When fragmented dispersal is combined with the staging behavior survival estimates in optimal-open territories could have considerable bias.

To the contrary, typical dispersal distances are short with individuals almost always staying within their natal population cluster (Breininger et al. 2006). It may be that undetected emigration was not a problem but rather that our results agree with (Woolfenden and Fitzpatrick

1984, Tringali and Bowman 2012, Sherer 2019) and are possibly a result of transitory extra-territorial forays in by young Scrub-Jays. This exploratory behavior may be informative to young jays but comes at the cost of elevated predation risk in unfamiliar surroundings and away from their kin and sentinel system (McGowan and Woolfenden 1989, Hailman et al. 1994) . Sherer (2019) found that individual juveniles prospecting in the spring preferentially used habitat similar to their natal territory during these forays, except for individuals from overgrown (suboptimal) territories. If this is the case in our study population, young Scrub-Jays from optimal-open territories could experience more interactions with dominant individuals during forays with increased risk of injury and perhaps lower survival.

The effect of age on survival, the trend of increasing survival over time in the unmarked and combined models, agrees with Woolfenden and Fitzpatrick's (1984) findings. The trend fits with the hypothesis that young Scrub-Jays are still developing foraging and predator avoidance skills. Jones at al. (2013) found that Scrub-jays recognized threats after the first contact with a new intruder. Similarly, Griesser and Suzuki (2017) found that young Siberian Jays only needed to witness mobbing by breeders and non-breeders once to identify predators and the recognition was permanent. Scrub-Jays have a structured sentinel system with participation from all adult family members; all family members immediately seek cover in response to robust alarm calls (Woolfenden and Fitzpatrick 1996). Griffin (2004) proposed social learning of predators was quick and durable in species with reliable alarm calls. We suggest that young Scrub-Jays fit this hypothesis.

Fitzpatrick and Bowman (2016) that found incremental increases in yearling production with up to 4 helpers inferring a positive effect on juvenile survival. These additional family members might provide more vigilance for young Scrub-Jays still learning predator avoidance.

However, helper numbers can interact with territory size because helpers can act as food competitors in small territories when young Scrub-Jays become independent (Mumme et al. 2015). While most of our study families had less than 4 helpers, we did not include territory size in our analysis because some territories overlapped private lands and territory size was not measurable. Because our analysis did not account for this complexity our results may be confounded. Mumme et al. (2015) studied Scrub-Jays in high quality homogenous habitat; our habitat quality varied and possibly contributed to a diminished helper effect. It is also possible that with 53% of our families having no helpers that sample sizes were not sufficient to detect a helper effect.

The effect directions of sibling count and cohort count were consistent with our hypotheses that naïve young Scrub-Jays may attract predators at a territory and larger territory cluster scale. This agrees with Griesser and Suzuki (2017) that found that juveniles in larger groups of the cooperatively breeding Siberian Jay (*Perisoreus infaustus*) had lower first winter survival than individuals in smaller groups. One possible explanation for this was that larger groups might be more easily detected by Goshawks (*Accipiter gentilis*) at the expense of inexperienced juveniles (Griesser and Suzuki 2017). An alternative explanation was that social interference from dominate breeders and non-breeders restricted subordinate juveniles to forage in areas with more predatory exposure (Nystrand 2006). We suggest Scrub-Jays encounter similar mechanisms related to aerial predation.

The negative effect of male breeder death agreed with our hypothesis that familial disruption would have negative consequences to juvenile family members. Breeding Florida Scrub-Jays form a tight monogamous bond and stay together until death of one of the pair; divorce is rare among Scrub-Jays (Woolfenden and Fitzpatrick 1984, 1996). Breeder death causes social disruption of the family unit and may prompt offspring (especially those of the same sex as the replacement breeder) to disperse (Goldstein et al. 1998) as a result of aggression from the replacement breeder (Fitzpatrick et al. 2016). We excluded sex from our analysis because we did not have a reliable method to determine sex of individuals during the capture period; sex is determined using observations of a vocalization given only by females, and some females do not give this call until later in life. Regardless of sex, we hypothesized that all juveniles would be especially sensitive to this disruption because of their low rank in the dominance hierarchy and reduced nepotism. The positive leaning effect of female breeder death is surprising with no realistic ecological explanation and could be spurious.

Conclusion

Our analysis of juvenile Scrub-Jays indicates a composite nature of the mechanisms that affect survival during this life stage. Combining datasets proved helpful in improving precision, reducing bias, and providing inference not possible from individual data sets. Habitat had the strongest effect on survival. Our estimates for habitat specific survival in optimal height territories were contrary to past work and may indicate a complex interplay of habitat structure, dominance hierarchies and dispersal behavior. Time presumably provides experience with predator avoidance and increased foraging efficiency and thus a positive effect on survival. Suggesting management actions based on our results alone would not be prudent but, when combined with past work, this study possibly reveals a benefit of optimal-closed habitat (i.e., high juvenile survival rates). It is important to note that currently only 20% of territories are optimal-open, far below the 70% recovery goal (Lacy and Breininger 2021). Creating more optimal-open territories is the priority but optimal-closed territories do not come with a cost to population viability and allow for a larger population (Lacy and Breininger 2021); our results bolster this notion but more work is needed to determine if large patches of optimal-closed are important for juvenile survival. Our prediction of male breeder death was also supported confirming the value of family cohesion in this cooperative breeder.

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Table 1. MCMC parameter estimates (posterior mean, standard error (SD) and 95% credible intervals) of the combined model show Florida Scrub-Jay juvenile survival increased with time and was positively affected by optimal territories (highest in optimal-closed) and is negatively affected by male death.

	Mean	**SD**	**2.50%**	**97.50%**
P(brood=1)	0.33	0.02	0.29	0.37
P(brood=2)	0.32	0.02	0.28	0.36
P(brood=3)	0.23	0.02	0.19	0.27
P(brood=4)	0.09	0.01	0.06	0.12
P(brood=5)	0.02	0.01	0.01	0.03
P(brood=6)	0.01	0.00	0.00	0.02
P(brood=7)	0.00	0.00	0.00	0.01
P(brood=8)	0.01	0.00	0.00	0.02
Phi intercept	2.56	0.29	2.02	3.15
Time	0.25	0.11	0.03	0.45
Time-squared	-0.02	0.02	-0.05	0.02
Optimal-closed (Phi)	0.98	0.28	0.44	1.55
Optimal-open (Phi)	0.58	0.25	0.10	1.08
p intercept unmarked	2.66	0.18	2.32	3.03
Optimal-closed (p) unmarked	-0.75	0.28	-1.30	-0.19
Optimal-open (p) unmarked	0.81	0.30	0.23	1.40
p intercept marked	3.95	0.37	3.28	4.73
Optimal-closed (p) marked	-0.69	0.43	-1.55	0.16

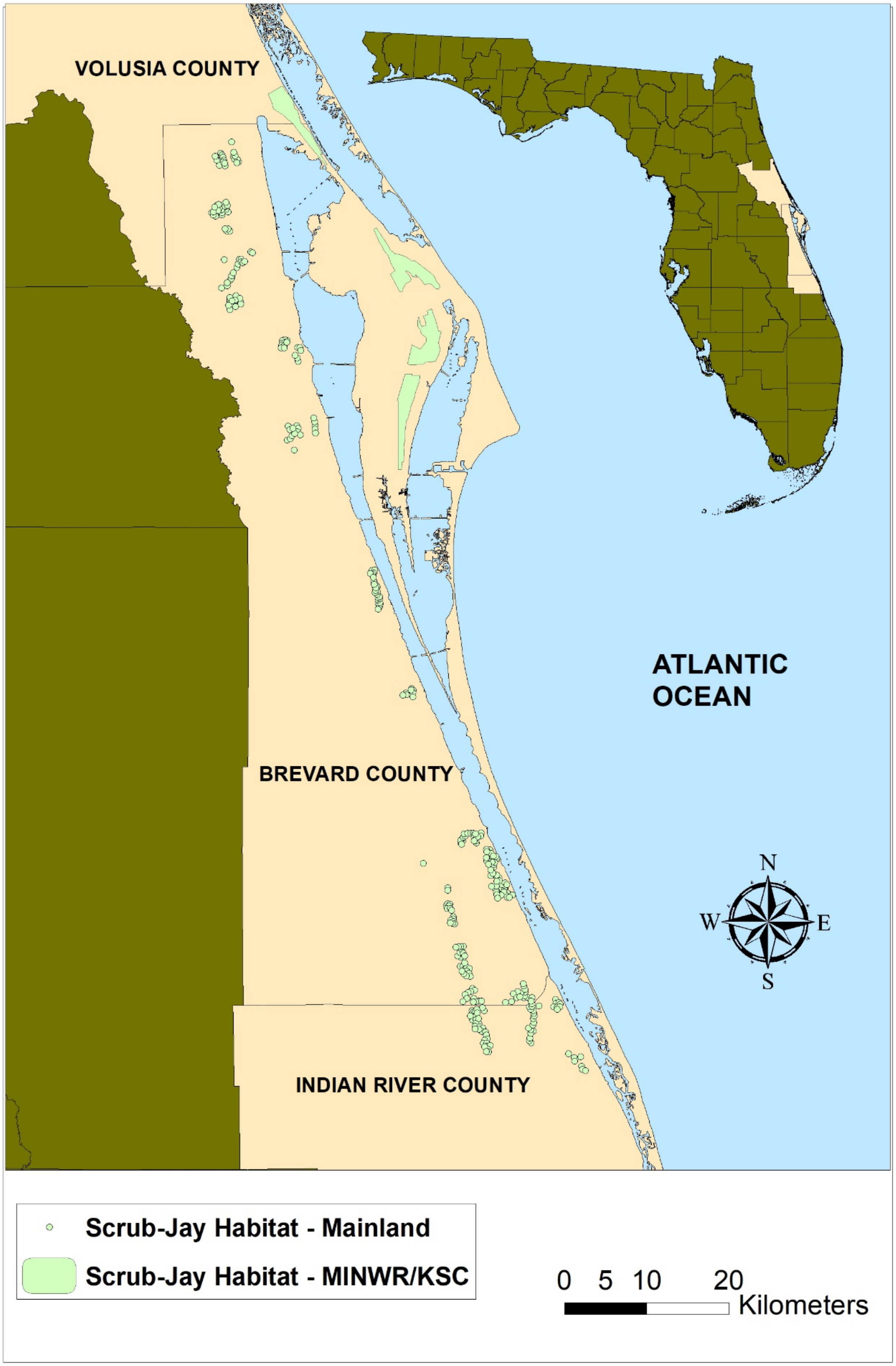
Optimal-open (p) marked	-0.54	0.35	-1.23	0.14
Female death	0.13	0.28	-0.42	0.69
Male death	-0.51	0.25	-1.00	-0.02
Helper count	-0.01	0.20	-0.40	0.40
Sibling count	-0.34	0.20	-0.74	0.06
Cohort count	-0.12	0.19	-0.50	0.26
Bayesian p-value marked data	0.70	0.46	0.00	1.00
Bayesian p-value unmarked data	0.73	0.44	0.00	1.00
sigma territory unmarked detection	2.28	0.13	2.05	2.55
sigma territory marked detection	2.08	0.27	1.60	2.66
sigma territory survival	2.00	0.18	1.68	2.37

Table 2. MCMC parameter estimates (posterior mean, standard error (SD) and 95% credible intervals) of the CJS model show Florida Scrub-Jay juvenile survival was highest in optimal-closed territories and is negatively affected by male death.

	Mean	**SD**	**2.50%**	**97.50%**
Phi intercept	4.17	1.09	2.51	6.70
Time	-0.30	0.30	-0.97	0.22
Time-squared	0.07	0.04	-0.01	0.16
Optimal-closed (Phi)	1.03	0.60	0.03	2.38
Optimal-open (Phi)	0.07	0.42	-0.77	0.92
p intercept	3.73	0.34	3.13	4.45
Optimal-closed (p)	-0.75	0.45	-1.66	0.13
Optimal-open (p)	-0.33	0.47	-1.26	0.59
Female death	-0.01	0.41	-0.79	0.86
Male death	-0.90	0.49	-1.99	-0.05
Helpercount	0.23	0.41	-0.49	1.15
Sibling count	-0.48	0.41	-1.37	0.25
Cohort count	-0.49	0.37	-1.29	0.19
Bayesian p-value data	0.40	0.49	0.00	1.00
sigma territory detection	2.07	0.27	1.58	2.66
sigma territory survival	1.54	0.78	0.12	3.15

Table 3. MCMC parameter estimates (posterior mean, standard error (SD) and 95% credible intervals) of the unmarked (dependent young) model show Florida Scrub-Jay juvenile survival increased with time and was highest in optimal-closed territories.

	Mean	**SD**	**2.50%**	**97.50%**
P(brood=1)	0.32	0.02	0.29	0.36
P(brood=2)	0.32	0.02	0.28	0.36
P(brood=3)	0.23	0.02	0.19	0.27
P(brood=4)	0.09	0.01	0.06	0.12
P(brood=5)	0.02	0.01	0.01	0.03
P(brood=6)	0.01	0.00	0.00	0.02
P(brood=7)	0.00	0.00	0.00	0.01
P(brood=8)	0.01	0.00	0.00	0.02
Phi intercept	2.25	0.32	1.64	2.91
Time	0.36	0.12	0.12	0.59
Time-squared	-0.03	0.02	-0.07	0.01
Optimal-closed (Phi)	1.04	0.34	0.40	1.73
Optimal-open (Phi)	0.77	0.30	0.19	1.38
p intercept	2.68	0.18	2.34	3.03
Optimal-closed (p)	-0.75	0.28	-1.30	-0.20
Optimal-open (p)	0.80	0.30	0.22	1.38
Female death	-0.01	0.35	-0.70	0.69
Male death	-0.36	0.30	-0.95	0.23
Helper count	-0.10	0.24	-0.57	0.37
Sibling count	-0.36	0.25	-0.86	0.11
Cohort count	-0.10	0.24	-0.57	0.37
Bayesian p-value	0.75	0.43	0.00	1.00
sigma territory detection	2.28	0.13	2.04	2.54
sigma territory survival	2.14	0.21	1.77	2.58


VOLUSIA COUNTY
BREVARD COUNTY
INDIAN RIVER COUNTY
ATLANTIC OCEAN
N
W
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Scrub-Jay Habitat - Mainland
Scrub-Jay Habitat - MINWR/KSC
0 5 10 20
Kilometers

647

Figure 1. East-Central Florida study sites including MINWR/KSC and mainland FL (28.919° N-27.648°N, 80.078°W-81.162°W).

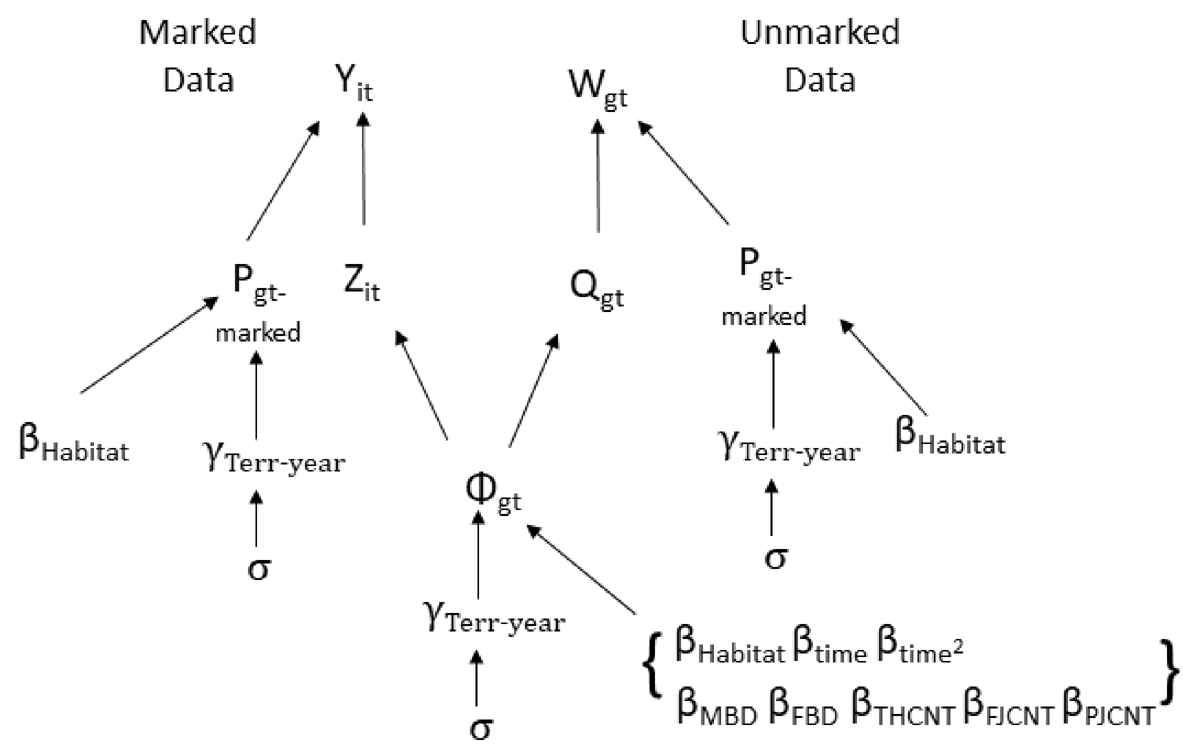

Figure 2. The integrated Bayesian hierarchical model of marked and unmarked juvenile Florida scrub-jay monthly survival and detection used observations of individually marked young ($Y_{i,t}$) and counts of unmarked young ($W_{g,t}$). Models for both data sets shared survival ($\Phi_{g,t}$) but had separate detection ($P_{g,t}$) parameters. Survival and detection parameters were modeled with covariates (β_{MD} = male death, β_{FD} = female death, β_{HC} = helper count, β_{SC} = sibling count, β_{CC} =

cohort count). There were also random effects of territory within year on survival and each detection parameter.

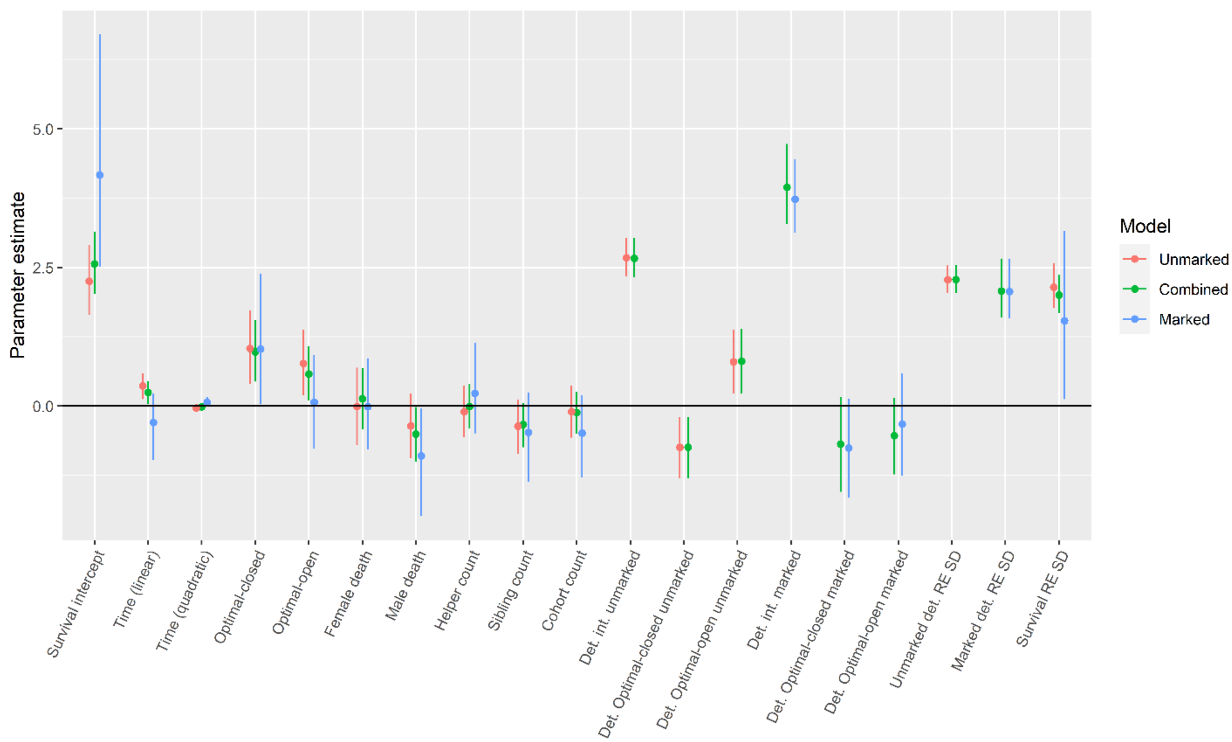

Figure 3. Parameter estimates of the combined model were intermediate between those of the individual dataset models. Key differences indicated higher survival within the marked data set, and differences in the time and habitat effects on survival. The larger unmarked data set had a larger influence on the combined model estimates. The points indicate the mean of the posterior distributions of parameter estimates and the bars give the 95 % credible intervals.

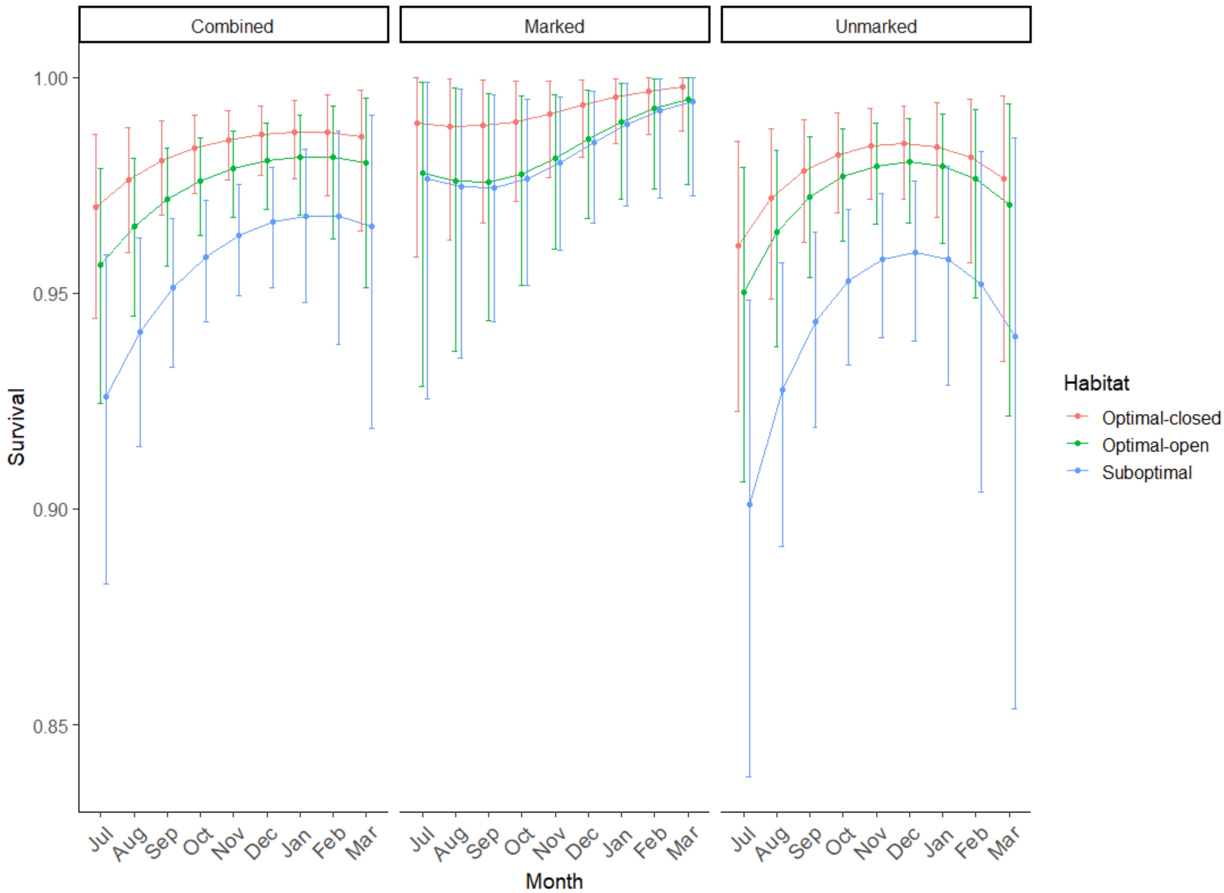

Figure 5. Survival vs time of the combined model more closely resembled the unmarked model and increased with time possibly suggesting young Scrub-Jays learning predator avoidance. The marked model did not show a trend. These estimates were calculated from the posterior beta estimates with all covariates other than month and habitat set at their mean values. We did not include the uncertainty due to the year random effect.

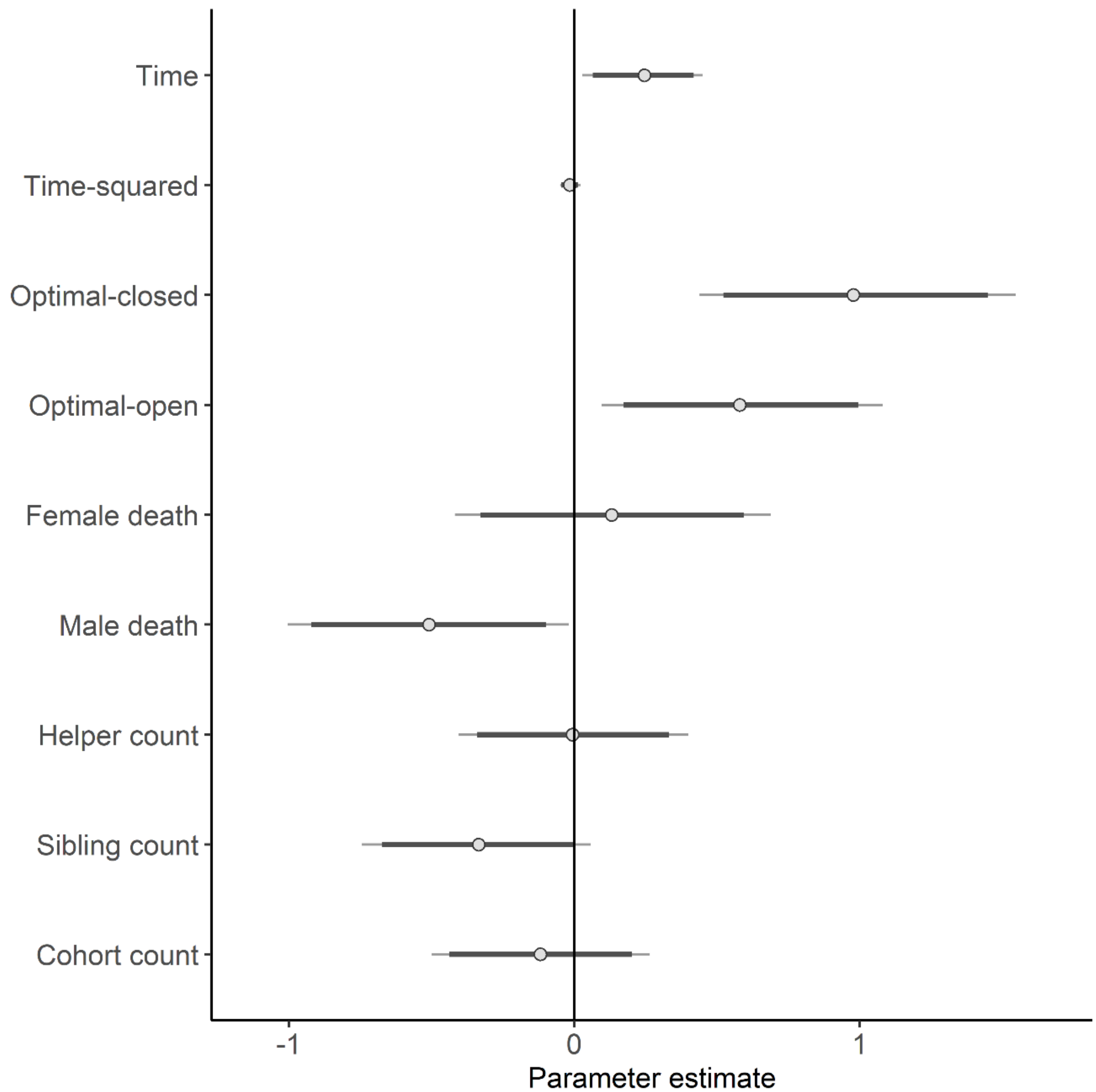

Figure 4. For the combined analysis optimal habitat had the largest positive effect, survival was highest in optimal-closed territories. Male death the largest negative effect on Scrub-Jay survival. Sibling count had a weak negative effect. The circles are the mean of posterior distribution of parameter estimates; thick bars are 90% and thin bars are 95% CI.

SUPPLEMENTAL MATERIAL

Combined Model Script

```
# Project.........: KSC/MINWR Florida-scrub Jay unmarked young survival
# Abstract........: Run hybrid RE model to convergence and get results models
# Author..........: Eric D. Stolen
# Created.........: February 13 2023
# Modified........:
# Data source.....:
# status..........:


#### Load required packages
require(tidyverse)
library(jagsUI)
library(ggmcmc)
library(coda)
library(bayesplot)

```

```
load("./RData//paper/FSJ_combined.RData")

# Hybrid RE  -----------------------------------------------------------

sink("./jags/combined seperate detection paper.jags")
cat("
model {

  ##  priors
  b0.phi ~ dnorm( 0, 0.01)
  beta.time.phi ~ dnorm( 0, 0.01)
  beta.time.sqr.phi~ dnorm( 0, 0.01)
  beta.weak ~ dnorm( 0, 0.01)
  beta.strong ~ dnorm( 0, 0.01)
  beta.BBFD ~ dnorm( 0, 0.01)
  beta.BBMD ~ dnorm( 0, 0.01)
  beta.THCNT ~ dnorm( 0, 0.01)
```

```
beta.FJCNT ~ dnorm( 0, 0.01)
beta.JJ ~ dnorm( 0, 0.01)
brood.probs[1:8]~ddirch(brood.probs.data)
b0.p.unmarked ~ dnorm( 0, 0.01)
beta.weak.p.unmarked ~ dnorm( 0, 0.01)
beta.strong.p.unmarked ~ dnorm( 0, 0.01)
b0.p.marked ~ dnorm( 0, 0.01)
beta.weak.p.marked ~ dnorm( 0, 0.01)
beta.strong.p.marked ~ dnorm( 0, 0.01)

# territory RE unmarked
for(i in 1:n.terr.year.unmarked){
  terr.unmarked.re[i] ~ dnorm(0, tau.terr.unmarked)
}
sigma.terr.unmarked ~ dnorm(0, 0.5)I(0,)    # hyperprior for RE sd
tau.terr.unmarked <- pow(sigma.terr.unmarked, -2)

# territory RE marked
```

```
for(i in 1:n.terr.year.marked){
  terr.marked.re[i] ~ dnorm(0, tau.terr.marked)
}
sigma.terr.marked ~ dnorm(0, 0.5)I(0,)        # hyperprior for RE sd
tau.terr.marked <- pow(sigma.terr.marked, -2)

# territory RE all
for(i in 1:n.terr.year){
  terr.all.re[i] ~ dnorm(0, tau.terr.all)
}
sigma.terr.all ~ dnorm(0, 0.5)I(0,)    # hyperprior for RE sd
tau.terr.all <- pow(sigma.terr.all, -2)

# linear model for combined survival
for( i in 1:nind.combined ){
  for( t in 1:(nocc-1) ){
    logit(phi[i,t]) <- b0.phi + beta.time.phi*t + beta.time.sqr.phi*(t-1)*(t-1) +
                    beta.strong*equals(Habitat[i],2) + beta.weak*equals(Habitat[i],3) +
```

```
                    beta.BBFD*BBFD[i] + beta.BBMD*BBMD[i] + beta.THCNT*THCNT[i] +
                    beta.FJCNT*FJCNT[i] + beta.JJ*JJ[i] +
                    terr.all.re[Terr.year.num[i]]
  }
}

# linear model for detection of unmarked
for( i in 1:n.terr.unmarked ){
  for( t in 1:nocc){
    logit(p.unmarked[i,t]) <- b0.p.unmarked + beta.weak.p.unmarked*equals(Habitat[i],3) +
    beta.strong.p.unmarked*equals(Habitat[i],2) +
    terr.unmarked.re[Terr.year.unmarked.num[i]]
  }
}
# linear model for detection of marked
for( i in 1:nind.marked ){
  for( t in 1:nocc){
    logit(p.marked[i,t]) <- b0.p.marked + beta.weak.p.marked*equals(Habitat[i+nind.marked],3)
+
```

```
    beta.strong.p.marked*equals(Habitat[i+nind.marked],2) +
    terr.marked.re[Terr.year.marked.num[i]]
  }
}


# likelihood for unmarked data
  for( i in 1:n.terr.unmarked ){
  w[i,1] ~ dcat(brood.probs[])
  w.new[i,1] ~ dcat(brood.probs[])
    cum.phi.um[i,1] <- 1
    for( t in 2:nocc ){
      # state
      w[i,t] ~ dbin( mu1[i,t], w[i,t-1])
      w.new[i,t] ~ dbin(mu1[i,t], w[i,t-1])
      mu1[i,t] <- phi[i, t-1]
      cum.phi.um[i,t]<-phi[i,t-1]*(cum.phi.um[i,t-1])
    }
```

```
    for( t in f.unmarked[i]:nocc ){
      # observation
      y.unmarked[i,t] ~ dbin( mu2[i,t], w[i,t])
      mu2[i,t] <- p.unmarked[i,t]
    }
  }

  # Posterior Predictive Check (Bayesian p-value) unmarked based on Schmidt et al. 2010
  for (i in 1: n.terr.unmarked){
    for(t in 2:nocc){
      w.new2[i,t] <- w.new[i,t]*pow(1-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t])) + (w.new[i,t-1]-w.new[i,t])*pow(0-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t]))
      w.2[i,t] <- w[i,t]*pow(1-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t])) + (w[i,t-1]-w[i,t])*pow(0-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t]))
      w.new2.FT[i,t] <- w.new[i,t]*pow(1-pow(cum.phi.um[i,t],0.5),2) + (w.new[i,t-1]-w.new[i,t])*pow(0-pow(cum.phi.um[i,t],0.5),2)
      w.2.FT[i,t] <- w[i,t]*pow(1-pow(cum.phi.um[i,t],0.5),2) + (w[i,t-1]-w[i,t])*pow(0-pow(cum.phi.um[i,t],0.5),2)
    }
```

```
  w.new3[i]<-sum(w.new2[i,2:nocc])
  w.3[i]<-sum(w.2[i,2:nocc])
  w.new3.FT[i]<-sum(w.new2.FT[i,2:nocc])
  w.3.FT[i]<-sum(w.2.FT[i,2:nocc])

}
w.new4<-sum(w.new3[1: n.terr.unmarked])
w.4<-sum(w.3[1: n.terr.unmarked])
P.unmarked<-step(w.new4-w.4)
w.new4.FT<-sum(w.new3.FT[1: n.terr.unmarked])
w.4.FT<-sum(w.3.FT[1: n.terr.unmarked])
P.unmarked.FT<-step(w.new4.FT-w.4.FT)


# Data Likelihood marked
for (i in 1:nind.marked){
 # Observation process
     cum.phi.m[i,f.marked[i]] <- 1
```

```
  for (t in (f.marked[i]+1):nocc){ # latent state at first capture given as data
    # State process
    Z.marked[i,t] ~ dbern(mu1.marked[i,t])
    Z.marked.new[i,t] ~ dbern(mu1.marked[i,t])
    # # Observation process
    mu1.marked[i,t] <- phi[n.terr.unmarked+i,t-1] * Z.marked[i,t-1]
    cum.phi.m[i,t]<-phi[n.terr.unmarked+i,t-1]*(cum.phi.m[i,t-1])
    # Observation process
    y.marked[i,t] ~ dbern(mu2.marked[i,t])
    mu2.marked[i,t] <- p.marked[i,t] * Z.marked[i,t]
    } #t
  } #i

 # Posterior Predictive Check (Bayesian p-value) marked based on Schmidt et al. 2010
   for (i in 1: nind.marked){
    for(t in (f.marked[i]+1):nocc){
      z.new2.m[i,t]<-pow(Z.marked.new[i,t]-cum.phi.m[i,t],2)/(cum.phi.m[i,t]*(1-cum.phi.m[i,t]))
      z.2.m[i,t]<-pow(Z.marked[i,t]-cum.phi.m[i,t],2)/(cum.phi.m[i,t]*(1-cum.phi.m[i,t]))
```

```
        z.new2.m.FT[i,t]<-pow(pow(Z.marked.new[i,t],0.5)-pow(cum.phi.m[i,t],0.5),2)
        z.2.m.FT[i,t]<-pow(pow(Z.marked[i,t],0.5)-pow(cum.phi.m[i,t],0.5),2)
      }
    z.new3.m[i]<-sum(z.new2.m[i,(f.marked[i]+1):nocc])
    z.3.m[i]<-sum(z.2.m[i,(f.marked[i]+1):nocc])
    z.new3.m.FT[i]<-sum(z.new2.m.FT[i,(f.marked[i]+1):nocc])
    z.3.m.FT[i]<-sum(z.2.m.FT[i,(f.marked[i]+1):nocc])
    }
  z.new4.m<-sum(z.new3.m[1: nind.marked])
  z.4.m<-sum(z.3.m[1: nind.marked])
  P.marked<-step(z.new4.m-z.4.m)
  z.new4.m.FT<-sum(z.new3.m.FT[1: nind.marked])
  z.4.m.FT<-sum(z.3.m.FT[1: nind.marked])
  P.marked.FT<-step(z.new4.m.FT-z.4.m.FT)

}
",fill = TRUE)
sink()
```

```
ch.init <- function(ch,f){
  z <- ch
  z[] <- NA
  occ <- dim(ch)[2]
  for( i in 1:dim(ch)[1] ){
    # browser()
    for(pos in 1:occ){
      if(pos == occ & is.na(ch[i,pos])){
        z[i,pos] <- z[i, pos-1]
      }else{
        if(all(is.na(ch[i,pos:occ]))){
          z[i,pos:occ] <- z[i, pos-1]
        }else{
          z[i,pos] <- max(ch[i,pos:occ],na.rm = T )
```

```
        }
      }
    }
  }
  return(z)
}

known.state.cjs <- function(ch){
  state <- ch
  state[] <- NA
  for (i in 1:dim(ch)[1]){
    n1 <- min(which(ch[i,]==1), na.rm = T)
    n2 <- max(which(ch[i,]==1), na.rm = T)
    state[i,n1:n2] <- 1
    # state[i,n1] <- NA
  }
  return(state)
}
```

```
cs.inits <- function(){
  list(
    w = ch.init(combined.data$y.unmarked,combined.data$f.unmarked),
    Z = known.state.cjs(combined.data$y.marked),
    b0.phi = runif(1, -3, 3),
    b0.p = runif(1, -3, 3)
  )
}



# run model -------------------------------------------------------------


cs.parms <- c("brood.probs","b0.phi", "beta.time.phi", "beta.time.sqr.phi", "beta.weak",
"beta.strong",
              "b0.p.unmarked", "beta.weak.p.unmarked", "beta.strong.p.unmarked",
              "b0.p.marked", "beta.weak.p.marked", "beta.strong.p.marked",
```

```
          "beta.BBFD", "beta.BBMD", "beta.THCNT","beta.FJCNT", "beta.JJ",
          "P.marked", "P.unmarked", "P.marked.FT", "P.unmarked.FT",
          "sigma.terr.unmarked", "sigma.terr.marked", "sigma.terr.all")

# load("./RData/hybrid_burnIn.RData")
nc=3
nt=1
n.iter=400
n.burnin=150

Hybrid.TerrSite.gof <- jags(data=c(combined.data), inits=cs.inits, parameters.to.save=cs.parms,
                    model.file = "./jags/combined seperate detection paper.jags",
                    n.chains = nc, n.thin = nt, n.iter = n.iter, n.burnin = n.burnin, parallel = TRUE)
print(Hybrid.TerrSite.gof, digits = 3)


Hybrid.TerrSite.gof.update <- update(Hybrid.TerrSite.gof, n.iter = 2000, parameters.to.save =
cs.parms)
print(Hybrid.TerrSite.gof.update, digits = 3)
```

```
Hybrid.TerrSite.gof.update.1 <- update(Hybrid.TerrSite.gof.update, n.iter = 4000,
parameters.to.save = cs.parms)
print(Hybrid.TerrSite.gof.update.1, digits = 3)

Hybrid.TerrSite.gof.update.2 <- update(Hybrid.TerrSite.gof.update.1, n.iter = 10000,
parameters.to.save = cs.parms)
print(Hybrid.TerrSite.gof.update.2, digits = 3)

Hybrid.TerrSite.gof.update.3 <- update(Hybrid.TerrSite.gof.update.2, n.iter = 10000,
parameters.to.save = cs.parms)
print(Hybrid.TerrSite.gof.update.3, digits = 3)

Hybrid.TerrSite.gof.update.4 <- update(Hybrid.TerrSite.gof.update.3, n.iter = 20000,
parameters.to.save = cs.parms)
print(Hybrid.TerrSite.gof.update.4, digits = 3)


out.jags.mcmc <- Hybrid.TerrSite.gof.update.4$samples
```

```
out.jags.mcmc <- as.mcmc.list(out.jags.mcmc)
out.jags.mcmc.thin <- window(out.jags.mcmc, thin=1)
S <- ggs(out.jags.mcmc.thin)
ggmcmc(S, file="./output/revisions 2/Hybrid BI plot1.pdf", plot=c("density", "traceplot", "running"))
ggmcmc(S, file="./output/revisions 2/Hybrid BI plot2.pdf", plot=c("compare_partial", "autocorrelation", "crosscorrelation", "Rhat", "geweke", "caterpillar"))


Hybrid.TerrSite.gof.update.5 <- update(Hybrid.TerrSite.gof.update.4, n.iter = 250000)
print(Hybrid.TerrSite.gof.update.5, digits = 3)
# write.csv(Hybrid.TerrSite.gof.update.2$summary, "./output/revisions/final_combined_posterior_estimates.csv")
save.image("./RData/hybrid_Final.RData")

Hybrid.TerrSite.gof.update.6 <- update(Hybrid.TerrSite.gof.update.5, n.iter = 250000)
print(Hybrid.TerrSite.gof.update.6, digits = 3)

save.image("./RData/hybrid_Final.RData")
```

```
posterior.tbl_eds <- function(Input, type="jagsUI"){
  # Input can be jagsUI model fit or mcmc.list object
  # library(runjags)
  # out.jags.mcmc <- combine.mcmc(list(out.2.update.3$samples, out.2.update.4$samples))

  require(coda)
  if(type=="jagsUI"){
    out.jags.mcmc <- Input$samples
  }else{
    out.jags.mcmc <- Input
  }
  # out.jags.mcmc <- jagsUI.fit$samples
  summary.tbl <- summary(out.jags.mcmc)
  size.tbl <- effectiveSize(out.jags.mcmc)
  GelRub <- gelman.diag(out.jags.mcmc,autoburnin=F, transform = T)
  out.tbl <- cbind(summary.tbl$statistics[,1:2],summary.tbl$quantiles[,c(1,3,5)],
                   Rhat=round(GelRub$psrf[,1],2), n.eff=round(size.tbl))
```

```
  print(out.tbl)
  return(out.tbl)
  # write.csv(out.tbl, "./output/revision final/HC_uninform_Posterior_summary.csv")
}


library(runjags)
out.hybrid.mcmc <- combine.mcmc(list(Hybrid.TerrSite.gof.update.5$samples,
                                     Hybrid.TerrSite.gof.update.6$sample))
                                    # Hybrid.TerrSite.gof.update.4$sample))
Hybrid.TerrSite.gof.tbl <- posterior.tbl_eds(out.hybrid.mcmc, type="list")

write.csv(Hybrid.TerrSite.gof.tbl, "./output/revisions 2/final_combined_posterior_estimates.csv")

out.hybrid.mcmc.ls <- as.mcmc.list(out.hybrid.mcmc)
out.hybrid.mcmc.ls.thin <- window(out.hybrid.mcmc.ls, thin=100)
S <- ggs(out.hybrid.mcmc.ls.thin)
```

```
ggmcmc(S, file="./output/revisions 2/Hybrid final plot1.pdf", plot=c("density", "traceplot",
"running"))
ggmcmc(S, file="./output/revisions 2/Hybrid final plot2.pdf", plot=c("compare_partial",
"autocorrelation", "crosscorrelation", "Rhat", "geweke", "caterpillar"))



# Plot BPV --------------------------------------------------------------



temp.params <- c("w.new4", "w.4", "z.new4.m", "z.4.m",
                 "w.new4.FT", "w.4.FT", "z.new4.m.FT", "z.4.m.FT")
# Hybrid.TerrSite.gof.3 <- update(Hybrid.TerrSite.gof.update.1, n.iter = 300, parameters.to.save
= temp.params)
Hybrid.TerrSite.gof.7 <- update(Hybrid.TerrSite.gof.update.6, n.iter = 10000, parameters.to.save
= temp.params)

Hybrid.TerrSite.gof.df <- with(Hybrid.TerrSite.gof.7$sims.list,
```

```
                    data.frame(New = c(w.new4,z.new4.m),
                          Data = c(w.4, z.4.m),
                          Submodel = factor(rep(c("unmarked", "marked"),
each=length(w.new4))),
                          RE="YearSiteTerr",
                    New.FT = c(w.new4.FT,z.new4.m.FT),
                    Data.FT = c(w.4.FT, z.4.m.FT))
                    )

(p.gof <- ggplot(Hybrid.TerrSite.gof.df, aes(y=New, x=Data)) + geom_point() +
  facet_wrap(~Submodel, scales = "free") + geom_abline(col="red") )
(p.gof.FT <- ggplot(Hybrid.TerrSite.gof.df, aes(y=New.FT, x=Data.FT)) + geom_point() +
    facet_wrap(~Submodel, scales = "free") + geom_abline(col="red") +
    xlab("Fit statistic for observed data") + ylab("Fit statistic for new data"))
(p.gof.FT.thin.fixed <-
ggplot(Hybrid.TerrSite.gof.df[sample(1:nrow(Hybrid.TerrSite.gof.df),1000),], aes(y=New.FT,
x=Data.FT)) + geom_point() +
    facet_wrap(~Submodel, scales = "fixed") + geom_abline(col="red") +
    xlab("Fit statistic for observed data") + ylab("Fit statistic for new data"))
```

```
(p.gof.FT.thin.free <-
ggplot(Hybrid.TerrSite.gof.df[sample(1:nrow(Hybrid.TerrSite.gof.df),1000),], aes(y=New.FT,
x=Data.FT)) + geom_point() +
    facet_wrap(~Submodel, scales = "free") + geom_abline(col="red") +
    xlab("Fit statistic for observed data") + ylab("Fit statistic for new data"))

pdf("./output/revisions 2/RE GOF plot Hybrid.pdf")
p.gof
p.gof.FT
dev.off()


ppi=600
tiff(file="./output/revisions 2/RE GOF plot Hybrid fixed.tiff",
     width = 6*ppi, height = 6*ppi, res = ppi)
p.gof.FT.thin.fixed
dev.off()

ppi=600
```

```
tiff(file="./output/revisions 2/RE GOF plot Hybrid free.tiff",
     width = 6*ppi, height = 6*ppi, res = ppi)
p.gof.FT.thin.free
dev.off()




# plot effects ------------------------------------------------------------

graph.labs <- c("Time", "Time-squared", "Optimal-closed", "Optimal-open",
                "Female death", "Male death", "Helper count", "Sibling count", "Cohort count")
attributes(out.hybrid.mcmc[[1]])$dimnames[[2]][c(10:13,20:24)] <- graph.labs
attributes(out.hybrid.mcmc[[2]])$dimnames[[2]][c(10:13,20:24)] <- graph.labs
attributes(out.hybrid.mcmc[[3]])$dimnames[[2]][c(10:13,20:24)] <- graph.labs
color_scheme_set(scheme="gray")

(plot.post.bar <- mcmc_intervals(out.hybrid.mcmc, point_est = "mean", prob = 0.9,
prob_outer=0.95,
```

```
                        pars = graph.labs, outer_size = 0.5, inner_size = 1,
                        point_size = 2) + theme_classic() + xlab("Parameter estimate") +
  # theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank()) +
  geom_vline(xintercept=0) + theme(axis.text = element_text(size = 11)))

ppi=600
tiff(file="./output/revisions 2/combined posterior CI for survival highres.tiff",
     width = 6*ppi, height = 6*ppi, res = ppi)
plot.post.bar
dev.off()

parameters.2 <- c("terr.unmarked.re", "terr.marked.re", "terr.all.re")
combinedYearRE.gof.4.plotRE <- update(Hybrid.TerrSite.gof.update.3,parameters.to.save =
parameters.2,  n.iter = 500)
S.all <- ggs(combinedYearRE.gof.4.plotRE$samples,family = "terr.all.re")
(plot.all <- ggs_caterpillar(S.all, line = 0, sort=T))
S.unmarked <- ggs(combinedYearRE.gof.4.plotRE$samples,family = "terr.unmarked.re")
(plot.unmarked <- ggs_caterpillar(S.unmarked, line = 0, sort=T))
S.marked <- ggs(combinedYearRE.gof.4.plotRE$samples,family = "terr.marked.re")
```

```
(plot.marked <- ggs_caterpillar(S.marked, line = 0, sort=T))
pdf(file="./output/revisions 2/caterpillar plots of RE.pdf")
plot.all
plot.unmarked
plot.marked
dev.off()
```

Marked Model Script

```
# Project.........: KSC/MINWR Florida-scrub Jay marked young survival

sink("./jags/FSJ survival Marked data only paper.jags")
cat("
model {
  ##  priors on logit scale probabilities
    b0.phi ~ dnorm( 0, 0.001)
    b0.p ~ dnorm( 0, 0.001)
    beta.time.phi ~ dnorm( 0, 0.001)
    beta.time.sqr.phi~ dnorm( 0, 0.001)
    beta.weak ~ dnorm( 0, 0.001)
    beta.strong ~ dnorm( 0, 0.001)
    beta.weak.p ~ dnorm( 0, 0.001)
    beta.strong.p ~ dnorm( 0, 0.001)
    beta.BBFD ~ dnorm( 0, 0.001)
    beta.BBMD ~ dnorm( 0, 0.001)
    beta.THCNT ~ dnorm( 0, 0.001)
```

```
beta.FJCNT ~ dnorm( 0, 0.001)
beta.JJ ~ dnorm( 0, 0.001)

## territory RE detection
for(i in 1:n.terr.year){
  re.terr.det[i] ~ dnorm(0, tau.terr.det)
}
sigma.terr.det ~ dnorm(0, 0.5)I(0,) # hyperprior for RE sd
tau.terr.det <- pow(sigma.terr.det, -2)

## territory RE survival
for(i in 1:n.terr.year){
  re.terr.phi[i] ~ dnorm(0, tau.terr.phi)
}
sigma.terr.phi ~ dnorm(0, 0.5)I(0,) # hyperprior for RE sd
tau.terr.phi <- pow(sigma.terr.phi, -2)

# set up linear models unmarked & unmarked
```

```
  for( i in 1:nind.marked ){
    for( t in 1:(nocc-1) ){
      logit(phi[i,t]) <- b0.phi + beta.time.phi*t + beta.time.sqr.phi*(t-1)*(t-1) +
                        beta.strong*equals(Habitat[i],2) + beta.weak*equals(Habitat[i],3) +
                        beta.BBFD*BBFD[i] + beta.BBMD*BBMD[i] + beta.THCNT*THCNT[i] +
                        beta.FJCNT*FJCNT[i] + beta.JJ*JJ[i] + re.terr.phi[Terr.year.num[i]]
    }
     for( t in 1:nocc){
      logit(p[i,t]) <- b0.p + beta.weak.p*equals(Habitat[i],3) + beta.strong.p*equals(Habitat[i],2)
+ re.terr.det[Terr.year.num[i]]
    }
  }

# Data Likelihood marked
for (i in 1:nind.marked){
    cum.phi.m[i,f.marked[i]] <- 1
   for (t in (f.marked[i]+1):nocc){ # latent state at first capture given as data
    # State process
    Z.marked[i,t] ~ dbern(mu1.marked[i,t])
```

```
      Z.marked.new[i,t] ~ dbern(mu1.marked[i,t])
      mu1.marked[i,t] <- phi[i,t-1] * Z.marked[i,t-1]
      cum.phi.m[i,t]<-phi[i,t-1]*(cum.phi.m[i,t-1])
      # Observation process
      y.marked[i,t] ~ dbern(mu2.marked[i,t])
      mu2.marked[i,t] <- p[i,t] * Z.marked[i,t]
      } #t
    } #i

 # Posterior Predictive Check (Bayesian p-value) marked based on Schmidt et al. 2010
    for (i in 1: nind.marked){
      for(t in (f.marked[i]+1):nocc){
        z.new2.m[i,t]<-pow(Z.marked.new[i,t]-cum.phi.m[i,t],2)/(cum.phi.m[i,t]*(1-cum.phi.m[i,t]))
        z.2.m[i,t]<-pow(Z.marked[i,t]-cum.phi.m[i,t],2)/(cum.phi.m[i,t]*(1-cum.phi.m[i,t]))
        z.new2.m.FT[i,t]<-pow(pow(Z.marked.new[i,t],0.5)-pow(cum.phi.m[i,t],0.5),2)
        z.2.m.FT[i,t]<-pow(pow(Z.marked[i,t],0.5)-pow(cum.phi.m[i,t],0.5),2)
      }
    z.new3.m[i]<-sum(z.new2.m[i,(f.marked[i]+1):nocc])
```

```
    z.3.m[i]<-sum(z.2.m[i,(f.marked[i]+1):nocc])
    z.new3.m.FT[i]<-sum(z.new2.m.FT[i,(f.marked[i]+1):nocc])
    z.3.m.FT[i]<-sum(z.2.m.FT[i,(f.marked[i]+1):nocc])

    }
  z.new4.m<-sum(z.new3.m[1: nind.marked])
  z.4.m<-sum(z.3.m[1: nind.marked])
  P.marked<-step(z.new4.m-z.4.m)
  z.new4.m.FT<-sum(z.new3.m.FT[1: nind.marked])
  z.4.m.FT<-sum(z.3.m.FT[1: nind.marked])
  P.marked.FT  <-step(z.new4.m.FT - z.4.m.FT)

}
",fill = TRUE)
sink()
```

```
# load data ------------------------------------------------------------

# Load required packages
require(tidyverse)
library(jagsUI)
library(ggmcmc)
library(coda)
library(bayesplot)

load(file="./RData//paper/FSJ_marked_only.RData")

ch.init <- function(ch,f){
  z <- ch
  z[] <- NA
  occ <- dim(ch)[2]
  for( i in 1:dim(ch)[1] ){
    # browser()
```

```
    for(pos in 1:occ){
      if(pos == occ & is.na(ch[i,pos])){
        z[i,pos] <- z[i, pos-1]
      }else{
        if(all(is.na(ch[i,pos:occ]))){
          z[i,pos:occ] <- z[i, pos-1]
        }else{
          z[i,pos] <- max(ch[i,pos:occ],na.rm = T )
        }
      }
    }
  }
  return(z)
}

known.state.cjs <- function(ch){
  state <- ch
  state[] <- NA
```

```
  for (i in 1:dim(ch)[1]){
    n1 <- min(which(ch[i,]==1), na.rm = T)
    n2 <- max(which(ch[i,]==1), na.rm = T)
    state[i,n1:n2] <- 1
    # state[i,n1] <- NA
  }
  return(state)
}

cs.inits <- function(){
  list(
    Z = known.state.cjs(combined.data.marked$y.marked),
    b0.phi = runif(1, -3, 3),
    b0.p = runif(1, -3, 3)
  )
}
```

```
cs.parms <- c("brood.probs","b0.phi", "beta.time.phi", "beta.time.sqr.phi", "beta.weak",
"beta.strong",
            "b0.p", "beta.weak.p", "beta.strong.p", "beta.BBFD",
            "beta.BBMD", "beta.THCNT","beta.FJCNT", "beta.JJ", "sigma.terr.det",
"sigma.terr.phi",
            "sigma.terr.det", "sigma.terr.phi", "P.marked.FT", "P.marked")

nc=3
nt=1
n.iter=400
n.burnin=150
Marked.out <- jags(data=combined.data.marked, inits=cs.inits, parameters.to.save=cs.parms,
                  model.file = "./jags/FSJ survival Marked data only paper.jags",
                  n.chains = nc, n.thin = nt, n.iter = n.iter, n.burnin = n.burnin, parallel = TRUE)
print(Marked.out, digits = 3)
```

```
Marked.out.update <- update(Marked.out, n.iter = 30000)
print(Marked.out.update, digits = 3)

out.jags.mcmc <- Marked.out.update$samples
out.jags.mcmc <- as.mcmc.list(out.jags.mcmc)
out.jags.mcmc.thin <- window(out.jags.mcmc, thin=10)
S <- ggs(out.jags.mcmc.thin)
ggmcmc(S, file="./output/revisions/Marked BI plot1.pdf", plot=c("density", "traceplot", "running"))
ggmcmc(S, file="./output/revisions/Marked BI plot2.pdf", plot=c("compare_partial", "autocorrelation", "crosscorrelation", "Rhat", "geweke", "caterpillar"))

Marked.out.update.2 <- update(Marked.out.update, n.iter = 200000)
print(Marked.out.update.2, digits = 3)
save.image(file="./RData/Marked only.RData")

Marked.out.update.3 <- update(Marked.out.update.2, n.iter = 200000)
print(Marked.out.update.3, digits = 3)
save.image(file="./RData/Marked only.RData")
```

```
Marked.out.update.4 <- update(Marked.out.update.3, n.iter = 500000)
print(Marked.out.update.4, digits = 3)
save.image(file="./RData/Marked only.RData")


posterior.tbl_eds <- function(Input, type="jagsUI"){
  # Input can be jagsUI model fit or mcmc.list object
  # library(runjags)
  # out.jags.mcmc <- combine.mcmc(list(out.2.update.3$samples, out.2.update.4$samples))

  require(coda)
  if(type=="jagsUI"){
    out.jags.mcmc <- Input$samples
  }else{
    out.jags.mcmc <- Input
  }
  # out.jags.mcmc <- jagsUI.fit$samples
```

```
  summary.tbl <- summary(out.jags.mcmc)
  size.tbl <- effectiveSize(out.jags.mcmc)
  GelRub <- gelman.diag(out.jags.mcmc,autoburnin=F, transform = T)
  out.tbl <- cbind(summary.tbl$statistics[,1:2],summary.tbl$quantiles[,c(1,3,5)],
                   Rhat=round(GelRub$psrf[,1],2), n.eff=round(size.tbl))
  print(out.tbl)
  return(out.tbl)
  # write.csv(out.tbl, "./output/revision final/HC_uninform_Posterior_summary.csv")
}


# unmarked.only.update.tbl <- posterior.tbl_eds(unmarked.out.update)
library(runjags)
out.unmarked.mcmc <- combine.mcmc(list(Marked.out.update.2$samples,
Marked.out.update.3$sample,
                                       Marked.out.update.4$samples))
marked.only.update.tbl <- posterior.tbl_eds(out.unmarked.mcmc, type="list")
```

```
out.jags.mcmc <- as.mcmc.list(out.unmarked.mcmc)
out.jags.mcmc.thin <- window(out.jags.mcmc, thin=100)
S <- ggs(out.jags.mcmc.thin)
ggmcmc(S, file="./output/revisions/Marked final plot1.pdf", plot=c("density", "traceplot",
"running"))
ggmcmc(S, file="./output/revisions/Marked final plot2.pdf", plot=c("compare_partial",
"autocorrelation", "crosscorrelation", "Rhat", "geweke", "caterpillar"))

write.csv(marked.only.update.tbl, file="./output/revisions 2/marked only posterior.csv")
save.image(file="./RData/Marked only.RData")
```

Unmarked Model Script

```
# Project.........: KSC/MINWR Florida-scrub Jay unmarked young survival


# jags model ------------------------------------------------------------
sink("./jags/FSJ survival unmarked data only paper.jags")
cat("
model {
  ##  priors on logit scale probabilities
    b0.phi ~ dnorm( 0, 0.001)
    b0.p ~ dnorm( 0, 0.001)
    beta.time.phi ~ dnorm( 0, 0.001)
    beta.time.sqr.phi~ dnorm( 0, 0.001)
    beta.weak ~ dnorm( 0, 0.001)
    beta.strong ~ dnorm( 0, 0.001)
    beta.weak.p ~ dnorm( 0, 0.001)
    beta.strong.p ~ dnorm( 0, 0.001)
    beta.BBFD ~ dnorm( 0, 0.001)
```

```
  beta.BBMD ~ dnorm( 0, 0.001)
  beta.THCNT ~ dnorm( 0, 0.001)
  beta.FJCNT ~ dnorm( 0, 0.001)
  beta.JJ ~ dnorm( 0, 0.001)
  brood.probs[1:8]~ddirch(brood.probs.data)

## territory RE detection
  for(i in 1:n.terr.year){
    re.terr.det[i] ~ dnorm(0, tau.terr.det)
  }
  sigma.terr.det ~ dnorm(0, 0.5)I(0,) # hyperprior for RE sd
  tau.terr.det <- pow(sigma.terr.det, -2)

  ## territory RE survival
  for(i in 1:n.terr.year){
    re.terr.phi[i] ~ dnorm(0, tau.terr.phi)
  }
  sigma.terr.phi ~ dnorm(0, 0.5)I(0,) # hyperprior for RE sd
```

```
tau.terr.phi <- pow(sigma.terr.phi, -2)

# set up linear models unmarked & unmarked
for( i in 1:n.terr.unmarked ){
  for( t in 1:(nocc-1) ){
    logit(phi[i,t]) <- b0.phi + beta.time.phi*t + beta.time.sqr.phi*(t-1)*(t-1) +
                    beta.strong*equals(Habitat[i],2) + beta.weak*equals(Habitat[i],3) +
                    beta.BBFD*BBFD[i] + beta.BBMD*BBMD[i] + beta.THCNT*THCNT[i] +
                    beta.FJCNT*FJCNT[i] + beta.JJ*JJ[i] + re.terr.phi[Terr.year.num[i]]
  }
   for( t in 1:nocc){
   logit(p[i,t]) <- b0.p + beta.weak.p*equals(Habitat[i],3) + beta.strong.p*equals(Habitat[i],2) +
                  re.terr.det[Terr.year.num[i]]
  }
}

# likelihood unmarked
for( i in 1:n.terr.unmarked ){
```

```
w[i,1] ~ dcat(brood.probs[])
w.new[i,1] ~ dcat(brood.probs[])
  cum.phi.um[i,1] <- 1
  for( t in 2:nocc ){
    # state
    w[i,t] ~ dbin( mu1[i,t], w[i,t-1])
    w.new[i,t] ~ dbin(mu1[i,t], w[i,t-1])
    mu1[i,t] <- phi[i, t-1]
    cum.phi.um[i,t]<-phi[i,t-1]*(cum.phi.um[i,t-1])
  }
  for( t in f.unmarked[i]:nocc ){
    # observation
    y.unmarked[i,t] ~ dbin( mu2[i,t], w[i,t])
    mu2[i,t] <- p[i,t]
  }
}

# Posterior Predictive Check (Bayesian p-value) unmarked based on Schmidt et al. 2010
```

```
  for (i in 1: n.terr.unmarked){
    for(t in 2:nocc){
      # w.new2[i,t] <- w.new[i,t]*pow(1-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t])) + (w.new[i,1]-w.new[i,t])*pow(0-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t]))
      # w.2[i,t] <- w[i,t]*pow(1-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t])) + (w[i,1]-w[i,t])*pow(0-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t]))
      w.new2[i,t] <- w.new[i,t]*pow(1-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t])) + (w.new[i,t-1]-w.new[i,t])*pow(0-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t]))
      w.2[i,t] <- w[i,t]*pow(1-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t])) + (w[i,t-1]-w[i,t])*pow(0-cum.phi.um[i,t],2)/(cum.phi.um[i,t]*(1-cum.phi.um[i,t]))
      w.new2.FT[i,t] <- w.new[i,t]*pow(1-pow(cum.phi.um[i,t],0.5),2) + (w.new[i,t-1]-w.new[i,t])*pow(0-pow(cum.phi.um[i,t],0.5),2)
      w.2.FT[i,t] <- w[i,t]*pow(1-pow(cum.phi.um[i,t],0.5),2) + (w[i,t-1]-w[i,t])*pow(0-pow(cum.phi.um[i,t],0.5),2)
    }
  w.new3[i]<-sum(w.new2[i,2:nocc])
  w.3[i]<-sum(w.2[i,2:nocc])
  w.new3.FT[i]<-sum(w.new2.FT[i,2:nocc])
  w.3.FT[i]<-sum(w.2.FT[i,2:nocc])
```

```
  }
  w.new4<-sum(w.new3[1: n.terr.unmarked])
  w.4<-sum(w.3[1: n.terr.unmarked])
  P.unmarked<-step(w.new4-w.4)
  w.new4.FT<-sum(w.new3.FT[1: n.terr.unmarked])
  w.4.FT<-sum(w.3.FT[1: n.terr.unmarked])
  P.unmarked.FT<-step(w.new4.FT-w.4.FT)

}
",fill = TRUE)
sink()


# load data ---------------------------------------------------------------

# Load required packages
require(tidyverse)
```

```
library(jagsUI)
library(ggmcmc)
library(coda)
library(bayesplot)

load(file="./RData//paper/FSJ_unmarked_only.RData")

ch.init <- function(ch,f){
  z <- ch
  z[] <- NA
  occ <- dim(ch)[2]
  for( i in 1:dim(ch)[1] ){
    # browser()
    for(pos in 1:occ){
      if(pos == occ & is.na(ch[i,pos])){
        z[i,pos] <- z[i, pos-1]
      }else{
        if(all(is.na(ch[i,pos:occ]))){
```

```
        z[i,pos:occ] <- z[i, pos-1]
      }else{
        z[i,pos] <- max(ch[i,pos:occ],na.rm = T )
      }
    }
  }
 }
 return(z)
}

known.state.cjs <- function(ch){
  state <- ch
  state[] <- NA
  for (i in 1:dim(ch)[1]){
    n1 <- min(which(ch[i,]==1), na.rm = T)
    n2 <- max(which(ch[i,]==1), na.rm = T)
    state[i,n1:n2] <- 1
    # state[i,n1] <- NA
```

```
  }
  return(state)
}

cs.inits <- function(){
  list(
    w = ch.init(combined.data.unmarked$y.unmarked,combined.data.unmarked$f.unmarked),
    # Z = known.state.cjs(combined.data$y.marked),
    b0.phi = runif(1, -3, 3),
    b0.p = runif(1, -3, 3)
  )
}


cs.parms <- c("brood.probs","b0.phi", "beta.time.phi", "beta.time.sqr.phi", "beta.weak",
"beta.strong",
              "b0.p", "beta.weak.p", "beta.strong.p", "beta.BBFD",
              "beta.BBMD", "beta.THCNT","beta.FJCNT", "beta.JJ", "sigma.terr.det",
"sigma.terr.phi",
```

```
            "P.unmarked.FT", "P.unmarked")

nc=3
nt=1
n.iter=400
n.burnin=100
unmarked.out <- jags(data=combined.data.unmarked, inits=cs.inits,
parameters.to.save=cs.parms,
                model.file = "./jags/FSJ survival unmarked data only paper.jags",
                n.chains = nc, n.thin = nt, n.iter = n.iter, n.burnin = n.burnin, parallel = TRUE)
print(unmarked.out, digits = 3)

unmarked.out.update <- update(unmarked.out, n.iter = 30000)
print(unmarked.out.update, digits = 3)

out.jags.mcmc <- unmarked.out.update$samples
out.jags.mcmc <- as.mcmc.list(out.jags.mcmc)
out.jags.mcmc.thin <- window(out.jags.mcmc, thin=10)
S <- ggs(out.jags.mcmc.thin)
```

```
ggmcmc(S, file="./output/revisions/Unmarked BI plot1.pdf", plot=c("density", "traceplot",
"running"))
ggmcmc(S, file="./output/revisions/Unmarked BI plot2.pdf", plot=c("compare_partial",
"autocorrelation", "crosscorrelation", "Rhat", "geweke", "caterpillar"))

unmarked.out.update.2 <- update(unmarked.out.update, n.iter = 100000)
print(unmarked.out.update.2, digits = 3)

unmarked.out.update.3 <- update(unmarked.out.update, n.iter = 500000)
print(unmarked.out.update.3, digits = 3)

unmarked.out.update.4 <- update(unmarked.out.update.3, n.iter = 500000)
print(unmarked.out.update.4, digits = 3)
save.image("./RData/unmarked model.RData")


posterior.tbl_eds <- function(Input, type="jagsUI"){
  # Input can be jagsUI model fit or mcmc.list object
  # library(runjags)
```

```
  # out.jags.mcmc <- combine.mcmc(list(out.2.update.3$samples, out.2.update.4$samples))

  require(coda)
  if(type=="jagsUI"){
    out.jags.mcmc <- Input$samples
  }else{
    out.jags.mcmc <- Input
  }
  # out.jags.mcmc <- jagsUI.fit$samples
  summary.tbl <- summary(out.jags.mcmc)
  size.tbl <- effectiveSize(out.jags.mcmc)
  GelRub <- gelman.diag(out.jags.mcmc,autoburnin=F, transform = T)
  out.tbl <- cbind(summary.tbl$statistics[,1:2],summary.tbl$quantiles[,c(1,3,5)],
                   Rhat=round(GelRub$psrf[,1],2), n.eff=round(size.tbl))
  print(out.tbl)
  return(out.tbl)
  # write.csv(out.tbl, "./output/revision final/HC_uninform_Posterior_summary.csv")
}
```

```
# unmarked.only.update.tbl <- posterior.tbl_eds(unmarked.out.update)
library(runjags)
out.unmarked.mcmc <- combine.mcmc(list(unmarked.out.update.4$samples,
unmarked.out.update.3$sample,
                                    unmarked.out.update.2$samples))
unmarked.only.update.tbl <- posterior.tbl_eds(out.unmarked.mcmc, type="list")


out.jags.mcmc <- as.mcmc.list(out.unmarked.mcmc)
out.jags.mcmc.thin <- window(out.jags.mcmc, thin=100)
S <- ggs(out.jags.mcmc.thin)
ggmcmc(S, file="./output/revisions/Unmarked final plot1.pdf", plot=c("density", "traceplot",
"running"))
ggmcmc(S, file="./output/revisions/Unmarked final plot2.pdf", plot=c("compare_partial",
"autocorrelation", "crosscorrelation", "Rhat", "geweke", "caterpillar"))

save.image("./RData/unmarked model.RData")
```

write.csv(unmarked.only.update.tbl, file="./output/revisions 2/unmarked only posterior.csv")

Data

```
$y.unmarked
   July August September October November December January February
1     3     0        NA       3        2        3       3        1
2     2     1        NA       2        2        2       2        2
3     1     1        NA       0       NA        1       1        1
4     4     4        NA       4       NA        4       2        4
5     2     2        NA       2       NA        2       2        2
6     1     1        NA       1       NA        1       1        1
7     3     2         2       3        3        2       3        3
8     2    NA         1       2       NA        0       2        2
9     1     0         1      NA        1        1       1        1
10    1     1         0       0        0        0       0        0
11    0     1        NA       1        1       NA       1        1
12    0     0        NA      NA        0        0       1       NA
14    1     0         0       1        0        1       1        1
15    0     0         0       0        2        1      NA        2
16    1    NA        NA       1        1       NA       0        1
17    3     0        NA       0        0        0       0        0
20    0     0         0      NA        1        1       1        1
21    1     0         1      NA        1        1       1        1
22    1     0        NA      NA       NA       NA       1        1
23    2     0        NA      NA       NA       NA       2        2
24    1     1        NA      NA       NA       NA       1        1
25   NA    NA         1       1        0        2       2        2
26    1    NA         0       0        0        0       0        0
27    1    NA         1       1        0        0       0        0
```

28	2	2	2	2	2	2	2	2
30	2	2	2	2	1	NA	2	2
33	1	2	1	2	NA	1	NA	1
34	NA	1	NA	NA	NA	NA	1	1
37	1	0	NA	0	0	1	NA	NA
44	1	1	1	NA	1	1	1	NA
45	NA	2	2	NA	0	2	NA	NA
46	1	NA	NA	NA	1	1	1	1
47	3	NA	NA	NA	3	3	3	3
48	3	NA	NA	NA	3	3	3	3
49	1	NA	1	1	1	1	1	1
50	3	NA	NA	2	NA	3	3	3
51	0	NA	NA	3	NA	0	1	0
52	3	2	NA	1	3	1	2	NA
53	4	4	NA	4	4	4	2	NA
54	2	1	NA	2	2	2	NA	2
55	1	1	0	NA	1	1	NA	1
56	4	3	2	2	4	3	1	1
57	1	1	0	0	NA	1	1	NA
58	3	3	0	2	NA	3	0	0
59	5	5	5	0	0	NA	NA	NA
60	3	0	NA	NA	NA	NA	0	NA
61	2	1	2	2	NA	NA	2	1
62	NA	1	2	2	0	NA	1	1
63	3	1	3	2	2	NA	NA	1
64	3	3	1	1	1	0	0	0
65	2	2	0	0	0	0	0	0
66	3	2	0	0	NA	NA	NA	NA

67	1	1	NA	1	1	1	NA	1
68	2	0	2	2	1	2	0	0
69	0	2	2	2	2	2	2	2
70	0	0	1	1	1	1	1	1
71	1	NA	NA	0	0	NA	NA	NA
72	1	1	NA	1	NA	NA	0	1
73	2	3	NA	2	2	0	3	3
74	1	1	NA	1	0	0	1	1
75	0	2	NA	NA	0	2	0	0
76	1	NA	NA	1	1	NA	NA	1
77	NA	0	2	2	2	2	2	2
78	0	1	1	1	0	0	0	0
79	2	0	NA	0	0	0	0	0
80	2	2	0	1	2	2	2	2
81	3	2	4	4	4	4	3	NA
82	1	0	0	0	NA	0	0	0
83	1	NA	0	NA	NA	0	NA	0
84	0	2	0	1	NA	1	1	1
85	3	3	2	2	NA	3	3	2
86	3	NA	2	0	2	2	2	2
87	2	2	2	2	2	2	2	2
88	1	1	1	1	1	1	0	0
89	0	0	1	0	0	1	1	0
90	3	0	0	2	NA	2	0	3
91	3	1	0	3	NA	NA	2	2
92	NA	NA	NA	NA	NA	1	0	0
93	2	2	NA	NA	NA	2	2	NA
94	1	1	NA	2	0	2	2	2

95	1	0	NA	0	0	0	0	1
96	0	NA	NA	1	NA	NA	1	NA
97	NA	1	NA	NA	NA	NA	0	NA
98	2	NA	NA	0	1	1	1	0
99	1	NA	NA	0	0	1	1	0
100	3	NA	NA	1	1	NA	0	0
101	2	NA	NA	1	0	NA	1	NA
102	1	1	1	1	NA	1	NA	NA
103	2	0	NA	2	NA	2	2	0
104	NA	0	0	0	NA	1	1	0
105	1	0	1	1	1	1	1	1
106	0	0	NA	1	0	0	1	0
107	1	NA	1	1	NA	1	NA	1
108	1	NA	NA	NA	0	NA	NA	NA
109	2	2	1	2	2	1	1	1
110	2	1	2	2	NA	2	2	2
111	3	3	NA	3	2	2	3	2
112	1	1	1	1	NA	1	0	1
113	1	0	0	0	NA	0	1	0
114	0	2	2	0	NA	NA	2	0
115	2	NA	1	1	2	NA	2	2
116	0	1	0	1	1	1	1	1
117	2	2	2	0	1	0	2	1
118	0	2	0	1	1	NA	1	1
119	1	0	0	0	0	NA	0	1
120	2	2	3	3	3	NA	2	2
121	1	1	3	3	3	2	2	2
122	2	0	0	0	0	0	0	0

123 3 3 1 0 NA 2 2 2

124 2 1 1 1 NA 2 NA NA

125 NA 1 1 NA NA 1 NA 0

March

1	2
2	2
3	1
4	0
5	0
6	1
7	NA
8	NA
9	1
10	0
11	1
12	1
14	1
15	2
16	1
17	0
20	1
21	0
22	0
23	0
24	0
25	0
26	0
27	0

1725	28	2
1726	30	1
1727	33	1
1728	34	1
1729	37	0
1730	44	0
1731	45	0
1732	46	1
1733	47	3
1734	48	3
1735	49	1
1736	50	1
1737	51	1
1738	52	2
1739	53	2
1740	54	0
1741	55	1
1742	56	1
1743	57	0
1744	58	0
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1780	94	2

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687 688 689 690 691 692 693 694 695 696 697 698 699 700 701 702 703 704

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  2   2   2   3   1   3   3   2   1   3   3   1   3   3   1   1   2   1
723 724 725 726 727 728 729 730 731 732 733 734 735 736 737 738 739 740
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