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ANALYZING AVIAN NEST SURVIVAL IN FORESTS AND GRASSLANDS: A COMPARISON OF THE MAYFIELD AND LOGISTIC-EXPOSURE METHODS

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Abstract. Several new methods for analyzing avian nest survival have been developed recently. To date, few tests have compared the performance of these new approaches with the traditional approach to nest survival analysis, the Mayfield method. To address this question, we used the Mayfield method to reanalyze data on avian nest survival from two published studies that employed the logistic-exposure approach, one of the Mayfield alternatives. We found that both approaches yielded nearly identical point estimates of daily nest survival, although the Mayfield estimates were less precise than estimates generated by the logistic-exposure models. Hypothesis tests conducted via the two different approaches also yielded generally similar results, although in one of the studies the Mayfield analysis failed to identify one of the significant covariates revealed by the logistic-exposure approach, apparently due to the imprecision of the Mayfield estimates. In sum, our results suggest that estimates of nest survival generated using the Mayfield estimator or its alternatives will be comparable, and that results of studies conducted using the Mayfield method should not be discounted. At the same time, our results reinforce the previously demonstrated advantages of alternatives such as the logistic-exposure approach: the ability to evaluate complex models of nest survival, consider individual and continuous covariates, and produce more precise estimates of daily nest survival.

Key Words: American Robin, *Calcarius ornatus,* Chestnut-collared Longspur, *Dendroica petechia,* grassland birds, logistic-exposure, Mayfield method, nest survival, riparian birds, *Turdus migratorius,* Yellow Warbler.

ANALIZANDO LA SOBREVIVENCIA DE NIDO EN BOSQUES Y PASTIZALES: UNA COMPARACIÓN DE LOS MÉTODOS MAYFIELD Y DE EXPOSICIÓN LOGÍSTICA

Resumen. Varios métodos para el análisis de la sobrevivencia de nidos de aves han sido desarrollados recientemente. A la fecha, pocas pruebas han comparado el funcionamiento de estos nuevos enfoques, con el enfoque tradicional de análisis de sobrevivencia de nido, el método Mayfield. Para tratar esta cuestión utilizamos el método Mayfield para reanalizar datos sobre sobrevivencia de nido, de dos estudios publicados que emplearon el enfoque de exposición logística, una de las alternativas Mayfield. Encontramos que ambos enfoques mostraron casi estimaciones de punto idénticas de sobrevivencia diaria de nido, a pesar de que las estimaciones Mayfield eran menos precisas que las estimaciones generadas por los modelos de exposición logística. Pruebas de hipótesis conducidas vía ambos enfoques también muestran en general los mismos resultados, a pesar que en uno de los estudios el análisis Mayfield falló al identificar una de las covarientes significativas revelada por el enfoque de exposición logística, aparentemente debido a la imprecisión de las estimaciones Mayfield. En resumen, nuestros resultados sugieren que estimaciones de sobrevivencia de nido generadas utilizando el estimador Mayfield o sus alternativas, serán comparables, y que los resultados de estudios conducidos utilizando métodos Mayfield no deberían ser descontinuados. De igual forma nuestros resultados refuerzan las ventajas anteriormente demostradas de alternativas tales como el enfoque de exposición logística: la habilidad de evaluar modelos complejos de sobrevivencia de nido, consideración de covariantes individuales y continuas, y la producción de estimaciones más precisas de sobrevivencia de nido diaria.

Most studies of avian nest survival address two distinct components: estimation of daily nest survival rates and tests of hypotheses about the causes of variation in daily nest survival. Until recently, the Mayfield (Mayfield 1961) method has been the de facto standard for estimating daily nest-survival rate, and was used widely in hypothesis testing. However, testing hypotheses with the Mayfield method requires making contrasts among groups of nests and thus the types of hypotheses that could be tested has been limited. Over the past several years, a handful of new methods for estimating and comparing rates of daily nest survival have been developed that address some of the limitations of the Mayfield method and offer the opportunity for more complex analyses of nest survival (Dinsmore et al. 2002, Nur et al. 2004, Rotella et al. 2004, Shaffer 2004a). Although the advantages of these new approaches have been well established, rarely addressed is the extent to which analyses conducted under these new approaches will yield results that differ from the Mayfield method (but see Jehle et al. 2004). Answering this question is important for at least two reasons.

First, although Mayfield's estimator of daily nest survival is ad hoc, it is an unbiased, maximum-likelihood estimator (Hensler and Nichols 1981) like the proposed alternatives. Furthermore, it is simple to calculate, as is the standard error of the estimator (Johnson 1979). In contrast, estimating daily nest survival under all of the proposed alternatives requires the use of more complex statistical tools (e.g., generalized linear modeling), an understanding of model-based inference, and may require the use of specialized software (e.g., program MARK; Dinsmore et al. 2002). Given that the Mayfield method is easier to implement, many investigators may wish to continue using it for estimation purposes or for hypothesis tests conducted on grouped data. Thus, it is useful to compare results and inferences gained through the Mayfield method and its alternatives. Do hypothesis tests conducted with the Mayfield method commonly yield equivalent results to more complex models evaluated using one of the alternative methods? Second, an extensive body of nest survival estimates generated using the Mayfield approach exists; understanding how estimates generated under the Mayfield method differ from estimates generated by alternative methods is important if results obtained under different analytic approaches are to be compared.

Several existing studies contain information that can be used to evaluate the similarity of estimates obtained under different approaches (Rotella et al. 2004; Shaffer 2004a; Winter et al. 2004, 2005a, b). Jehle et al. (2004) addressed this question explicitly by comparing site-, year-, and stage-specific estimates of Lark Bunting (*Calamospiza melanocorys*) nest survival generated by the Mayfield method, the nest-survival module in program MARK (Dinsmore et al. 2002), and the method described by Stanley (2000, 2004a), and found that the estimates generated by different methods were nearly identical. Here, we add to this existing information by comparing estimates of daily nest survival and the results of hypothesis testing completed under the Mayfield method and the logistic-exposure approach (Shaffer 2004a). We chose to evaluate the logistic-exposure approach in particular as an alternative to the Mayfield estimator for several reasons. First, it has been widely adopted in studies of avian nesting success (Peak et al. 2004; Winter et al. 2004, 2005a, b); second, it is identical or comparable to other linear-modeling approaches in terms of both the estimates it generates and the way in which it evaluates independent variables (Rotella et al. 2004, Shaffer 2004a); and finally, it has not been included in previous comparisons with the Mayfield estimator (but see results in Shaffer 2004a; Winter et al. 2004, 2005a, b).

The Mayfield method and the logistic-exposure approach are fundamentally different in how they treat estimation and comparison of daily nest survival rates. In particular, the logistic-exposure approach relies on evaluating the strength of support for linear combinations of variables assembled into a set of candidate models. The best-supported model is generally used for estimation purposes, and the strength of all variables considered is addressed by evaluating odds ratios, which can be averaged across all models. In contrast, the Mayfield method relies on categorical comparisons among variables rather than a model-based approach to inference. Thus, directly parallel contrasts of the two methods are difficult to obtain. To compare the two approaches, we reanalyzed data presented in two existing studies of avian nest survival with the goal not only of comparing estimates of nest survival generated by Mayfield and the logistic-exposure approach, but also of addressing in a more general fashion how methodological choices influence the results of hypothesis tests. Each study addressed a different question of importance to avian ecologists, and each study was conducted in a different environment. These two studies are also useful in that one (Lloyd and Martin 2005) was focused primarily on comparing a categorical variable (native vs. exotic habitat), whereas the independent variables of interest in the other (Tewksbury et al. 2006) were both categorical (presence of a habitat buffer) and continuous (percent of agriculture in the landscape). Lloyd and Martin (2005) compared nest survival of Chestnut-collared Longspurs (*Calcarius ornatus*) in native and exotic grasslands, and Tewksbury et al. (2006) addressed the influence of landscape features on nest survival of birds breeding in western riparian forests. Both studies used the logistic-exposure approach to analyze nest survival; we reanalyzed the data using the Mayfield estimator to examine how the choice of an analytical method might influence study results.

METHODS

Full methodological details can be found in the original studies (Lloyd and Martin 2005, Tewksbury et al. 2006). Both studies estimated daily nest survival (probability that a nest survives a given day) and tested hypotheses about the causes of variation in daily nest survival using the generalized-linear-modeling approach of Shaffer (2004a). Hypotheses regarding variation in nest survival were tested by examining support, as indicated by Akaike's information criterion (AIC), for a set of candidate models (Burnham and Anderson 2002) that reflected the authors' assessment of likely causes of variation in nest survival. Lloyd and Martin (2005) were interested primarily in estimating habitat-specific reproductive success of Chestnut-collared Longspurs breeding in native prairie and non-native grasslands dominated by crested wheatgrass (*Agropyron cristatum*). The goal of the research was to address the possible link between the spread of exotic grasses, the loss of native prairie, and the decline of grassland birds. However, in addition to examining the effect of breeding habitat, they also examined the influence of year, nest age, date of nest initiation, and clutch size on daily nest survival. The authors considered 15 different combinations of these variables.

Tewksbury et al. (2006) addressed the general question of how landscape features influence rates of nest predation and brood parasitism. They collected data at 22 study sites along two river systems in the western US (the Bitterroot River and Snake River). Study sites were patches of riparian forest that were embedded within an agricultural landscape. Some sites were buffered from agriculture by remnant woodlands, whereas other sites were immediately adjacent to various agricultural lands. Tewksbury et al. (2006) used the logistic-exposure approach to examine the effect of two landscape variables—buffering (whether a site was buffered from agriculture) and the percent of each 1 km landscape surrounding the study sites that was under active agriculture. In addition to these variables, they examined the effects of nest age and date of nest initiation. Based on combinations of these variables, they built a candidate set of nine models.

Nest Survival of Chestnut-collared Longspurs in Native and Exotic Habitat

To investigate how the logistic-exposure approach and the Mayfield method differ in a hypothesis-testing context, we calculated odds ratios for each of the parameters included in the best supported model of Lloyd and Martin (2005). The parameters in the best-supported model included all of the parameters that Lloyd and Martin (2005), using model-averaged estimates, found to be important predictors of nest survival. We calculated 95% confidence intervals around each odds ratio, and interpreted those that did not overlap 1 as having significant effects on nest survival. We then used chi-square tests, implemented by program CONTRAST (Hines and Sauer 1989), to conduct parallel comparisons using the Mayfield estimator.

To compare point estimates of daily nest survival obtained using the two analytical approaches, we first took the best-supported model from Lloyd and Martin (2005) and used it to estimate daily nest survival in each habitat. Because the best-supported model included effects of three covariates (nest age, year, and clutch size; see Results), we used an iterative process in which appropriate values were entered for each covariate (i.e., all possible combinations of nest age, year, and clutch size). Estimates of daily nest survival thus obtained were averaged to produce a single estimate for each habitat. We also estimated nest survival using a model that included only an effect of habitat, which, although unsupported by the data in the analysis of Lloyd and Martin (2005), provides the most direct comparison with the Mayfield method. We then compared these two estimates to estimates of daily nest survival obtained using the traditional Mayfield method (Mayfield 1961, Johnson 1979). We recognize that collapsing the information derived from the best-fitting model is somewhat contrived, yet we also feel that it adequately addresses our question and provides important information on how the two estimation methods perform.

Nest Survival of Riparian Birds

Tewksbury et al. (2006) were interested in estimating daily nest survival of riparian birds in habitat patches that were either buffered or unbuffered from adjacent agricultural lands and that were situated in landscapes that differed in the proportion of land under agricultural production. Because one of the main covariates of interest (percent agriculture in the landscape) was continuous, comparing the performance of the Mayfield and logistic-exposure approaches required a somewhat different approach than required for Lloyd and Martin (2005).

To address the question using the logistic-exposure approach, we reanalyzed the data presented in Tewksbury et al. (2006) by comparing a subset of their candidate set of models. We evaluated four models that included combinations of the following variables: presence/absence of a buffer, percent of agriculture in the landscape, age of the nest, date of nest initiation, and a term reflecting the interaction between buffers and the percent of agriculture in the landscape. We used data from two species, Yellow Warblers

(*Dendroica petechia*) and American Robins (*Turdus migratorius*). We calculated odds ratios for each parameter in the best-supported model, 95% confidence intervals around each odds ratio, and interpreted those that did not overlap 1 as having significant effects on nest survival.

To address the question using the Mayfield method, we first calculated Mayfield estimates (Mayfield 1961) with standard errors (Johnson 1979) for each species at each study site. We then used the Mayfield estimates in an ANCOVA, with the presence of a buffer as a fixed factor and the percent of agriculture in the landscape as a covariate. We also examined the interaction between the presence of a buffer and the percent of agriculture in the landscape. Non-significant interaction terms were eliminated from analysis.

In addition to comparing the results of hypothesis tests conducted with the Mayfield method and the logistic-exposure approach (Shaffer 2004a), we also compared point estimates of daily nest survival generated by the two methods. We calculated point estimates for each site by adding a site dummy variable to the best-fitting logistic-exposure model and using the LSMEANS command. Point estimates of daily nest survival calculated by both approaches were then compared using Pearson's correlation coefficient

RESULTS

Nest Survival of Chestnut-collared Longspurs in Native and Exotic Habitat

The best-fitting model in Lloyd and Martin (2005) contained all variables except for nest initiation date, and was strongly supported relative to all other models (Akaike weight = 0.67). The model that included only an effect of habitat, which is comparable to the Mayfield comparison of reproductive success in the two habitats, received virtually no support (ΔAIC_c = 94.7, Akaike weight = 0). The logistic-regression equation for the best model (one standard error in parentheses) was:

$$\text{Logit}(\hat{S}_i) = \underset{(0.09)}{3.20} - \underset{(0.07)}{0.18}\,(\text{habitat}) + \underset{(0.0001)}{0.0001}\,(\text{year}) + \underset{(0.10)}{0.27}\,(\text{clutch size}) - \underset{(0.005)}{0.04}\,(\text{nest age})$$

Based on odds ratios calculated from parameter estimates in the best-fitting model, clutch size had the strongest effect on nest success, with each additional egg producing a 30% increase in the odds of a nest surviving a given day (odds ratio = 1.3, CL = 1.1, 1.6). The odds of daily survival decreased 4% per day over the course of the nesting period (odds ratio = 0.96, CL = 0.95, 0.97). Finally, the odds of daily nest survival were 17% greater in native habitat than in exotic habitat (odds ratio = 0.83, CL = 0.72, 0.96). The odds of a year effect (odds ratio = 1.0, CL = 1.0, 1.0) did not differ from that expected by random chance alone.

Results obtained by re-analyzing the same data set using the Mayfield method were somewhat similar. Daily nest survival varied significantly between the two habitats (χ^2 = 3.19, P = 0.07), and daily nest survival varied among nesting stages (laying = 0.84, incubation = 0.96, nestling = 0.94; χ^2 = 16.16, P <0.001). However, unlike the best-fitting model in the logistic-exposure analysis, which predicted a linear decrease in daily nest survival as a function of age, the Mayfield analysis indicated highest survival during the incubation period with slightly lower survival during the nestling period and extremely low survival during the laying period. As with the logistic-exposure analysis, yearly variation in nest survival was discountable (χ^2 = 0.30, P = 0.58). Clutch size, which was the strongest predictor of variation in nest survival in the logistic-exposure analysis, did not have a significant effect on nest survival (χ^2 = 2.74, P = 0.25) when evaluated using the Mayfield estimator. In examining the point estimates produced by the Mayfield estimate, there was evidence that nests with a clutch size of three had lower rates of daily nest survival (0.934, CL = 0.910, 0.958) than did nests with either four eggs (0.956, CL = 0.946, 0.966) or five eggs (0.956, CL = 0.940, 0.972). The lack of a statistically significant result appears to stem from the broad confidence intervals, especially for daily survival estimates for three-egg clutches.

Both methods produced similar estimates of daily nest survival in native and exotic habitat with broadly overlapping 95% confidence intervals (Table 1). Although point estimates of daily nest survival were almost identical, the confidence interval around the Mayfield estimator was much broader than for either of the estimates generated by the logistic-exposure approach.

Nest Survival of Riparian Birds

The best-fitting models in the reanalysis of American Robin and Yellow Warbler data from Tewksbury et al. (2006) contained all variables, and in both cases the best-fitting model was heavily supported by the data relative to the other models (Tables 2 and 3). In neither case was there strong evidence for an interaction between the presence of a buffer and the

TABLE 1. DAILY SURVIVAL RATE (95% CONFIDENCE LIMITS) OF CHESTNUT-COLLARED LONGSPUR NESTS IN NATIVE AND EXOTIC HABITAT, AS ESTIMATED BY THE MAYFIELD METHOD AND THE LOGISTIC-EXPOSURE METHOD.

	Estimator		
Habitat	Mayfield	Logistic-exposure (habitat only model)	Logistic-exposure (best model)
Native	0.954 (0.933, 0.957)	0.957 (0.953, 0.960)	0.954 (0.950, 0.959)
Exotic	0.945 (0.944, 0.963)	0.946 (0.941, 0.951)	0.946 (0.941, 0.951)

TABLE 2. SUMMARY OF AKAIKE'S INFORMATION CRITERION (AIC_c) VALUES FOR CANDIDATE MODELS EXPLAINING NEST SURVIVAL OF AMERICAN ROBINS IN THE SNAKE AND BITTERROOT RIVERS, AS GENERATED BY THE LOGISTIC-EXPOSURE APPROACH. *K* IS THE NUMBER OF PARAMETERS ESTIMATED BY THE MODEL, ΔAIC_c IS THE DIFFERENCE BETWEEN A GIVEN MODEL AND THE MODEL WITH THE LOWEST ΔAIC_c SCORE[a], AND AIC_c WEIGHT REFLECTS THE RELATIVE SUPPORT FOR EACH MODEL.

Model	*K*	ΔAIC_c	AIC_c weight
$S_{buffer+ agriculture+age+start date}$	5	0	0.74
$S_{buffer*agriculture+age+start date}$	5	2.8	0.18
$S_{buffer+age+start date}$	4	4.7	0.07
$S_{agriculture+age+start date}$	4	15.3	0.01

[a] The lowest AIC_c score was 2,397.9.

TABLE 3. SUMMARY OF AKAIKE'S INFORMATION CRITERION (AIC_c) VALUES FOR CANDIDATE MODELS EXPLAINING NEST SURVIVAL OF YELLOW WARBLERS IN THE SNAKE AND BITTERROOT RIVERS, AS GENERATED BY THE LOGISTIC-EXPOSURE APPROACH. *K* IS THE NUMBER OF PARAMETERS ESTIMATED BY THE MODEL, ΔAIC_c IS THE DIFFERENCE BETWEEN A GIVEN MODEL AND THE MODEL WITH THE LOWEST ΔAIC_c SCORE[a], AND AIC_c WEIGHT REFLECTS THE RELATIVE SUPPORT FOR EACH MODEL.

Model	*K*	ΔAIC_c	AIC_c weight
$S_{buffer+ agriculture+age+start date}$	5	0	0.79
$S_{buffer*agriculture+age+start date}$	5	2.6	0.21
$S_{buffer+age+start date}$	4	32.6	0.00
$S_{agriculture+age+start date}$	4	69.5	0.00

[a] The lowest AIC_c score was 3,882.8.

percent of agriculture. The logistic-regression equation for the best model (one standard error in parentheses) of American Robin daily nest survival was:

$$\underset{}{\text{logit}}(\hat{S}_i) = \underset{(0.623)}{3.49} - \underset{(0.143)}{0.633}\text{ (buffer)} - \underset{(0.056)}{0.17}\text{ (agriculture)} - \underset{(0.106)}{0.007}\text{ (age)} + \underset{(0.003)}{0.005}\text{ (start date)}$$

The logistic-regression equation for the best model (one standard error in parentheses) of Yellow Warbler daily nest survival was:

$$\text{logit}(\hat{S}_i) = \underset{(0.671)}{1.10} - \underset{(0.109)}{0.916}\text{ (buffer)} - \underset{(0.062)}{0.036}\text{ (agriculture)} - \underset{(0.103)}{0.016}\text{ (age)} + \underset{(0.004)}{0.023}\text{ (start date)}$$

For both species, site-specific point estimates of daily survival as estimated by the best-fitting model were highly correlated with point estimates generated using the Mayfield method (American Robin, $r^2 = 0.999$, $P < 0.001$; Yellow Warbler, $r^2 = 0.992$, $P < 0.001$; Fig. 1).

Odds ratios calculated from parameter estimates in the best-fitting model indicated a strong negative effect of natural habitat buffers in both species (American Robin, odds ratio = 0.53, CL = 0.40, 0.70; Fig. 2a; Yellow Warbler, odds ratio = 0.40, CL = 0.32, 0.50; Fig. 3a). Odds ratios also indicated a strong negative effect of the percentage of agriculture in the landscape on daily nest survival for American Robins (odds ratio = 0.84, CL = 0.76, 0.94), and a somewhat weaker negative effect for Yellow Warblers (odds ratio = 0.96, CL = 0.95, 0.98). The odds of an effect of the age of the nest were not different from that expected by random chance for either species. Start date had no effect on daily nest survival of American Robins, but did co-vary

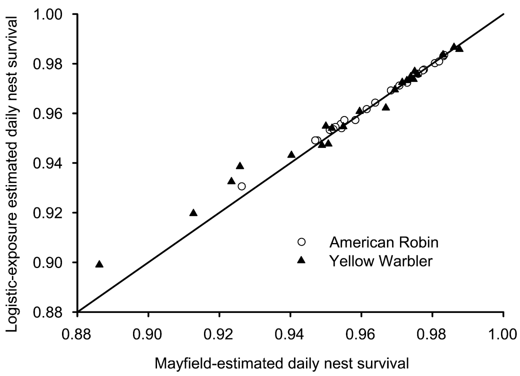

FIGURE 1. Estimates of daily nest survival generated by the Mayfield method and the logistic-exposure approach are nearly identical for both American Robin (r^2 = 0.999, P<0.001) and Yellow Warbler (r^2 = 0.992, P <0.001).

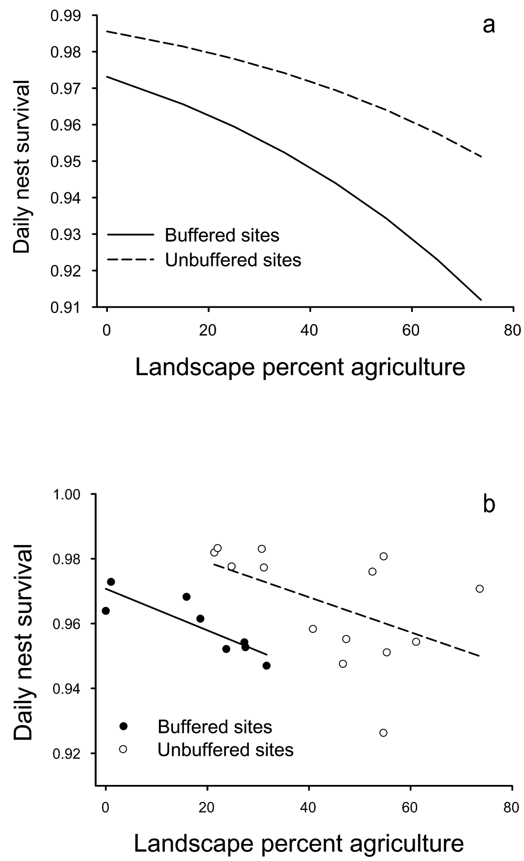

FIGURE 2. Both the best-fitting model from the logistic-exposure analysis (a) and the site-specific Mayfield estimates (b) indicated that daily nest survival of American Robins declined as the amount of agriculture in the landscape increased, and that daily nest survival was lower in sites buffered from surrounding agriculture by remnant woodland habitat. Mean population values for nest age and date of nest initiation were used to solve the logistic-regression equation and generate the curves.

positively with daily nest survival of Yellow Warblers (odds ratio = 1.02, CL = 1.02–1.03).

The ANCOVAs based on the Mayfield estimates for each site yielded somewhat different results. For American Robins, the presence of a natural habitat buffer (F = 8.2, df = 1, P = 0.01) and the percent of agriculture in the landscape (F = 8.6, df = 1, P = 0.01) both significantly affected daily nest survival (Fig. 2b). The interaction between buffer and agriculture was not significant (F = 0.05, df = 1, P = 0.84). For Yellow Warblers, the presence of a woodland buffer did not significantly affect daily nest survival (F = 1.24, df = 1, P = 0.28) but the percent of agriculture in the landscape had a significant negative effect on daily nest survival (F = 26.69, df = 1, P < 0.001; Fig. 3b). In addition, the interaction between agriculture and buffer was significant for Yellow Warblers (F = 10.16, df = 1, P = 0.005). The effect of woodland buffers appears to increase as the amount of agriculture in the landscape increases; buffers appeared to result in decreased daily nest survival at all sites except for those embedded in landscapes with a low percentage of agriculture. The ANOVA model of American Robins daily nest survival explained relatively little variation (adjusted r^2 = 0.28), whereas the Yellow Warbler ANOVA model explained substantially more (adjusted r^2 = 0.65).

DISCUSSION

In our reanalysis of two studies of avian nest survival, we compared the performance of the Mayfield method and the logistic-exposure approach, one of a class of similar methods that are based in generalized linear modeling, in estimating rates of daily nest survival and testing hypotheses about the causes of variation in these rates. In both studies, estimates of daily nest survival generated under the two approaches were nearly identical. This is not a surprising result as the Mayfield estimator, like the logistic-exposure approach, is a maximum-likelihood estimator. Several other studies also have reported little difference in daily nest survival as estimated by the Mayfield method and several of its alternatives, including the logistic-exposure approach (Shaffer 2004a; Winter et al. 2004, 2005a, b), the PROC NLMIXED model (Rotella et al. 2004), program MARK (Dinsmore et al. 2002), and the method developed by

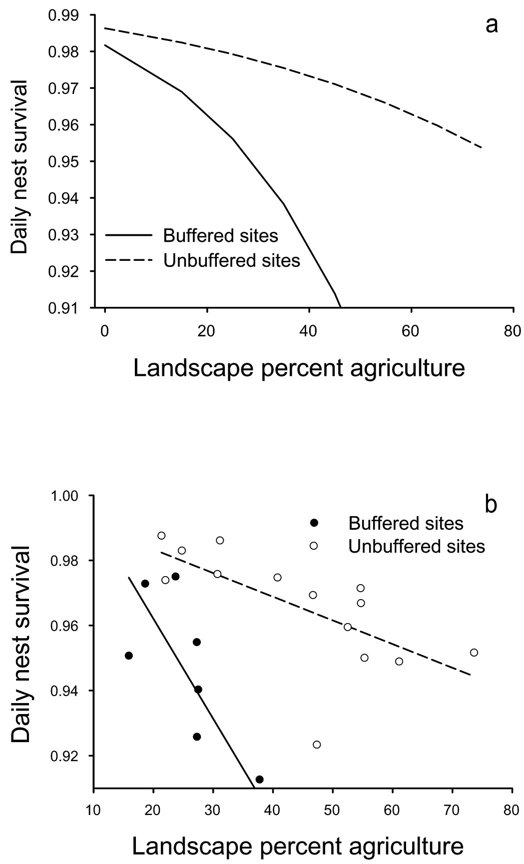

FIGURE 3. Both the best-fitting model from the logistic-exposure analysis (a) and the site-specific Mayfield estimates (b) indicated that daily nest survival of Yellow Warblers declined as the amount of agriculture in the landscape increased, and that daily nest survival was lower in sites buffered from surrounding agriculture by remnant woodland habitat. Mean population values for nest age and date of nest initiation were used to solve the logistic-regression equation and generate the curves.

Stanley (2000, 2004a, Jehle et al. 2004). However, an important caveat of our finding, and similar findings in the previously cited studies, is that the comparison of point estimates generated under the two approaches required collapsing large amounts of information from the logistic-exposure model to generate a single mean that could be compared to the point estimate generated by the Mayfield method. For example, to compare estimates of daily nest survival of Chestnut-collared Longspurs in native and exotic habitat, we had to calculate point estimates of daily nest survival for all possible combinations of habitat, clutch size, nest age, and year, the variables included in the best logistic-exposure model. We then averaged these values to arrive at a single estimate for each habitat for comparison with the Mayfield estimate. This effectively eliminates much of the additional information gained by using a generalized-linear-modeling approach. At the same time, the similarity of estimates of daily survival generated by the Mayfield method and the habitat-only model of Lloyd and Martin (2005) suggests that the Mayfield method and its alternatives will produce comparable estimates when the same covariates are considered. However, in this case, the Mayfield estimate was substantially less precise than estimates of daily nest survival generated from the logistic-exposure models.

Our comparison of hypothesis testing under the Mayfield method and the logistic-exposure approach yielded mixed results. In the re-analysis of Lloyd and Martin (2005), the principal finding was similar regardless of the method used to compare rates of daily nest survival—Chestnut-collared Longspurs in the exotic habitat had lower rates of daily nest survival. The Mayfield method and the logistic-exposure approach also indicated that daily nest survival varied depending upon the age of the nest. However, the two approaches differed in the predicted form of this relationship. The Mayfield analysis, which by its nature was limited to comparisons among stages of nesting, indicated that survival was lowest during egg laying, increased during incubation, and decreased slightly during the nestling period. In contrast, nest age was modeled as a linear function in the logistic-exposure analysis, and thus predicted a linear decline in nest survival from laying to fledging. This does not reflect an inherent flaw in the logistic-exposure approach, but rather points to the importance of including models that accurately reflect biological reality. For example, Lloyd and Martin (2005) might have better modeled the relationship between daily nest survival and nest age using a quadratic function, rather than the apparently over-simplistic linear model. Investigators who adopt the philosophy of model-based inference must keep in mind that the best model in a weak set of candidate models generates only weak inference.

Lloyd and Martin (2005) also reported that clutch size had the strongest effect on daily nest survival of Chestnut-collared Longspurs, with nests of larger clutch size having higher daily survival rates. In contrast, the re-analysis using the Mayfield method indicated that daily nest survival was constant among nests of different clutch size; this appeared to be a result of the large standard errors associated with the survival estimates for three-egg clutches. Although the failure to detect an effect of clutch size did not affect the conclusions drawn about the quality of the native and exotic habitats (clutch size is identical in both habitats), it does reveal how the reduced precision of Mayfield estimates can limit the power to detect differences among groups of nests. In this case, using the logistic-exposure approach revealed an interesting relationship that would have gone undetected with the Mayfield method.

The reanalysis of the data in Tewksbury et al. (2006) indicated broad similarities in the results of hypothesis tests conducted under the two approaches. The logistic-exposure approach suggested support for a negative effect of both natural habitat buffers and the percent of agriculture in the landscape on daily nest survival of American Robins and Yellow Warblers. These results lend support to the additive-predation model of Tewksbury et al. (2006), which suggests that nest predation rates are a product of both forest-dwelling predators close to the study site and generalist agricultural predators acting at larger spatial scales. The reanalysis of these data using site-specific Mayfield estimates of daily nest survival also suggested a significant negative effect of natural habitat buffers for both species, and a significant negative effect of agriculture. In the ANCOVA model for Yellow Warblers, buffers as a main effect were not significant, but the significant interaction between buffers and agriculture suggests a relationship similar to that predicted by the logistic-exposure analysis. In landscapes with little agriculture, buffers are relatively unimportant predictors of daily nest survival. However, as the amount of agriculture in the landscape increases, the effect of agriculture on daily nest survival increasingly depends upon the presence of a woodland buffer. Thus, for both species, the Mayfield method also provided support for the additive-predation model.

Several caveats should be kept in mind regarding our findings. First, we have not conducted a formal meta-analysis, and our results are based on a reanalysis of data presented in two studies, neither of which was chosen randomly. However, we felt these studies were useful for re-analysis because they addressed commonly asked questions in avian ecology, they were conducted in two different environments and with different species, and they were interested in the effect of fundamentally different covariates of daily nest survival (a categorical habitat variable in Lloyd and Martin [2005], and a mix of categorical and continuous variables in Tewksbury et al. [2006]). Second, although we found that both methods produced nearly identical point estimates of daily nest survival, comparing estimates from the best-fitting model in the logistic-exposure analysis with Mayfield estimates required collapsing much of the unique information obtained from the logistic-exposure approach. Finally, our comparison does not address instances in which the logistic-exposure and related methods are the only appropriate way to analyze data, e.g., modeling patterns of daily variation in nest survival (Grant et al. 2005).

Despite these caveats, we believe that the results presented here have important implications for the analysis of nest-survival data. First, they suggest that Mayfield estimates and estimates obtained under alternative approaches will be similar. This is important for analyses that seek to synthesize multiple existing estimates of daily nest survival from the literature, such as for meta-analyses or range-wide comparisons of reproductive success. Second, in some cases, the choice of an analytical method will not influence the results of hypothesis tests. In the studies presented here, both the Mayfield method and the logistic-exposure analysis yielded similar conclusions, although the results were not identical. The only substantive difference was that the analysis of the Mayfield estimates from Lloyd and Martin (2005) did not indicate a significant effect of clutch size on daily nest survival, whereas the logistic-exposure analysis revealed clutch size to be the strongest predictor of variation in nest survival. Also, the ANCOVA on Mayfield estimates from Tewksbury et al. (2006) suggested an interaction between buffers and agriculture for Yellow Warblers, whereas the interaction model tested with the logistic-exposure analysis received relatively little support. However, the significance of the interaction term had little bearing on the conclusions drawn: under both analytical approaches, American Robins and Yellow Warblers experienced lower daily nest survival rates in buffered sites and in landscapes dominated by agriculture. Nonetheless, the differences that we observed between results generated by the two methods suggest that, in some cases, conclusions may be dependent on the choice of an analytical method.

That the results of the Mayfield method and its alternatives are often comparable should not be construed as an argument for or against a particular mode of analysis. Other authors (Dinsmore et al. 2002, Nur et al. 2004, Rotella et al. 2004, Shaffer 2004a) have clearly established the drawbacks and limitations of both the Mayfield method and its alternatives. Many of the recently developed approaches for modeling avian nest survival offer the ability to test new hypotheses about avian nest survival or more robustly address existing hypotheses that have been limited to flawed tests using ad hoc approaches (see examples in Rotella et al. 2004). They also offer the opportunity to ask more interesting questions about nest survival, and to build models that may better reflect biological reality. The Mayfield alternatives, such as logistic exposure, allow more precise estimates of nest survival, and thus can offer increased power to detect patterns obscured by the chi-square tests used to compare Mayfield estimates. The linear-modeling process exploited by the Mayfield alternatives also allows investigators to estimate the effect of changes in one independent variable while holding all other independent variables constant. Thus, the Mayfield alternatives may allow better control over potentially confounding relationships among independent variables. At the same time, our results suggest that results obtained via the Mayfield method may not be substantively different from results obtained using one of the Mayfield alternatives. The Mayfield method, with its ease of application, remains a reasonable choice for estimation purposes or for the analysis of grouped data. Finally, with the increased flexibility offered by the Mayfield alternatives comes an increased obligation to carefully consider the variables that are included in candidate models. The questions asked concerning avian nest survival, and the variables measured to address those questions, must still come from theory and logic, and not from faith that more powerful analytical techniques alone will yield novel insights into causal relationships.

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