Do fluctuating water levels alter nest survivorship in reservoir shrubs?

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RESEARCH ARTICLE

Do fluctuating water levels alter nest survivorship in reservoir shrubs?

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ABSTRACT

Reservoirs often have highly fluctuating water levels. The perimeters of these impoundments, which alternate between being exposed or inundated by water (drawdown zone), are used by nesting birds, but at the risk of nest submergence when water levels rise. For species that nest above the ground in shrubs, foraging and predation may also be affected by flooded habitat. Our objective was to clarify the net impact that habitat flooding has on nest survivorship at Arrow Lakes Reservoir, British Columbia, Canada. This reservoir typically shows a pattern of water management where water is stored during the spring snowmelt (increasing water levels) and released later in the year. Yellow Warblers (*Setophaga petechia*; $n = 272$ nests) and Willow Flycatchers (*Empidonax traillii*; $n = 81$ nests) nested in similar parts of the drawdown zone, but differences in their nesting behaviors, particularly timing of nesting, caused the flycatchers to experience more nest submergence. Flycatchers also nested on a floating island of bog habitat, offering them some protection from nest submergence. We found little evidence that drawdown zone shrubs functioned as ecological traps. In flooded conditions, 28% of warbler nests failed due to submergence. Warbler nest daily survival rate (DSR) declined with advancing ordinal date, and we concluded that their DSR was not influenced by habitat flooding. For flycatchers, 50% of nest failures were caused by submergence under flooded conditions, but DSR did not differ between flooded (0.960 ± 0.009) and unflooded conditions (0.958 ± 0.012). We speculate that these counterintuitive results may be explained by a reduction in predation levels during flooded conditions, which may compensate for nest submergence. Finally, we found that nest DSR was enhanced in the floating island habitat (0.986 ± 0.005), indicating that floating habitat islands can be highly productive and may hold potential as a management tool for enhancing productivity of reservoir drawdown zones.

Keywords: reservoir operations, reservoir ecology, drawdown zone, riparian habitat, Willow Flycatcher, *Empidonax traillii*, Yellow Warbler, *Setophaga petechia*

Les fluctuations du niveau d'eau altèrent-elles la survie des nids dans les arbustes en bordure de réservoir?

RÉSUMÉ

Les réservoirs subissent souvent de grandes fluctuations du niveau d'eau. Le périmètre de ces réservoirs, lequel alterne entre exposé et inondé par l'eau (zone de rabattement), est utilisé par les oiseaux nicheurs, mais au risque que leur nid soit submergé lorsque le niveau d'eau s'élève. Pour les espèces qui nichent au-dessus du sol dans les arbustes, la quête alimentaire et la prédation peuvent également être affectées par l'inondation de l'habitat. Notre objectif était de clarifier l'impact net de l'inondation de l'habitat sur la survie du nid à l'Arrow Lakes Reservoir, en Colombie-Britannique. Ce réservoir présente typiquement un patron de gestion de l'eau avec une élévation du niveau d'eau après la fonte des neiges printanière et une baisse du niveau d'eau plus tard en été. *Setophaga petechia* ($n = 272$ nids) et *Empidonax traillii* ($n = 81$ nids) ont niché dans des parties similaires de la zone de rabattement, mais des différences dans leur comportement nicheur, particulièrement la chronologie de nidification, ont entraîné plus de submersion des nids chez *E. traillii*. Ceux-ci ont également niché sur une tourbière flottante, qui leur offrait une certaine protection contre la submersion des nids. Nous avons trouvé peu de preuves que les arbustes de la zone de rabattement fonctionnaient comme des trappes écologiques. Dans des conditions d'inondation, 28 % des nids de *S. petechia* ont échoué en raison de leur submersion. Le taux de survie quotidien (DSR) de *S. petechia* a diminué avec l'avancement de la date ordinale, et nous avons conclu que leur DSR n'était pas influencé par l'inondation de l'habitat. Pour *E. traillii*, 50 % des échecs de nidification ont été causés par la submersion lors de conditions d'inondation, mais le DSR des nids ne différait pas entre des conditions d'inondation (0,960 ± 0,009) et de non-inondation (0,958 ± 0,012). Nous supposons que ces résultats contre-intuitifs sont expliqués par une réduction des niveaux de prédation lors des conditions d'inondation, ce qui compense pour la submersion des nids. Finalement, nous avons trouvé que le DSR des nids était amélioré dans l'habitat flottant (0,986 ± 0,005), indiquant que les

habitats des îles flottantes peuvent être très productifs et présenter un potentiel comme outil de gestion pour augmenter la productivité des zones de rabattement des réservoirs.

Mots-clés: exploitation de réservoir, écologie de réservoir, zone de rabattement, habitat riverain, survie du nid, DSR, *Empidonax traillii*, *Setophaga petechia*

INTRODUCTION

More than half of the world's large river systems are regulated by an estimated 16.7 million impoundments (Nilsson et al. 2005, Lehner et al. 2011), with ~50,000 of these being major reservoirs, behind dams >15 m in height (Berga et al. 2006). The impoundment of valleys for the purposes of irrigation, flood control, and power generation is responsible for considerable loss of riparian and other valley habitat (Baxter 1977, Nilsson and Dynesius 1994, Nilsson et al. 2005). Yet, despite impoundment, remnant habitats often remain within reservoir drawdown zones—the periodically submerged perimeter topography that lies between the minimum and maximum reservoir water surface elevations.

The potential for drawdown zone habitats to support wildlife is particularly important for serially impounded rivers where very little riparian or wetland habitat remains outside the combined reservoir footprint. Reservoir drawdown zones can support substantial amounts of riparian vegetation (Rains et al. 2004, Hatten et al. 2010), but the value of these habitats for wildlife is unclear. The nature of drawdown zone habitats varies considerably among impoundments according to reservoir operations. In drier climates, water levels may fluctuate widely among years in large impoundments that cannot reliably be filled to maximum capacity each year, leading to dynamic vegetation conditions over time (e.g., Hatten et al. 2010). In wet climates, impoundments are more likely to be filled to near maximum capacity annually during rainy seasons or by the spring freshet (high discharge of rivers caused by snowmelt), and drained during the remainder of the year. This latter, more predictable type of operation can lead to a stable, graded profile of vegetation communities across drawdown zone elevations, with the distribution of each plant species reflecting its tolerance to being submerged. In either scenario, shrubs can become established or retained in drawdown zones.

Drawdown zone shrub growth is known to provide important nesting habitat for at least one endangered passerine, the Southwestern Willow Flycatcher (*Empidonax traillii extimus*; Ellis et al. 2009). Yet, there is concern that drawdown zones may function as ecological traps for birds that attempt to nest in them (Espie et al. 1998, Desgranges et al. 2006, Anteau et al. 2012). Considerable research has previously examined water level management in marshes, with a focus on waterfowl, marsh birds, shorebirds, and habitat selection (e.g., Wolf 1955, Rundle

and Fredrickson 1981, Parsons 2002, Baschuk et al. 2012). Reservoir ecology is still in its infancy, and the impacts of reservoirs on birds remain poorly understood (Calvert et al. 2013).

Reservoir drawdown zones are highly modified and unpredictable as nesting habitat, leading to the possibility that they may function as ecological traps (Robertson and Hutto 2006). Drawdown zones may function as ecological traps not only through the intrinsic fact of being human-altered habitat (Robertson and Hutto 2006, Quinlan and Green 2012), but also specifically because water may inundate nesting areas during the nesting period. Rising water leads directly to reproductive failure due to nest submergence (Espie et al. 1998, Desgranges et al. 2006, Anteau et al. 2012). Nest submergence is a particularly serious issue for ground-nesting species, which experience ~100% nest failure when their nesting habitats become flooded (but see Wiltermuth et al. 2009). Nest flooding may also threaten shrub-nesting species, especially in wet climates where drawdown zone shrubs can become flooded annually.

In addition to submerging nests, rising water levels transform terrestrial habitat into aquatic habitat, with probable effects on both food availability and predation pressure at nests that escape submergence owing to their elevated position above the ground (i.e. in shrubs); these impacts could be positive or negative depending on how food availability and predation pressure are altered. Nest predation is often low in aquatic or inundated habitats (Picman et al. 1993, Cain et al. 2003, Hoover 2006, Roy Nielsen and Gates 2007, Robertson and Olsen 2015), and some nest predators are known to avoid inundated habitats (Cocimano et al. 2011). The potential for multiple, and possibly opposing, effects of habitat flooding on nest survivorship complicates expectations regarding the impacts of reservoir operations on shrub-nesting birds, making it challenging to understand the value of drawdown zone shrubs as nesting habitat.

In this study we examined the nesting ecology and the impact of reservoir operations on the nesting performance of two shrub-nesting species, the Yellow Warbler (*Setophaga petechia*) and the Willow Flycatcher (*Empidonax traillii*; hereafter 'warbler' and 'flycatcher,' respectively), both of which nest in the drawdown zone of the Arrow Lakes Reservoir in southeastern British Columbia, Canada. Specifically, we compared the locations and heights of their nests, the timing of their nesting, and the occurrence of nest failure due to submergence, and examined how
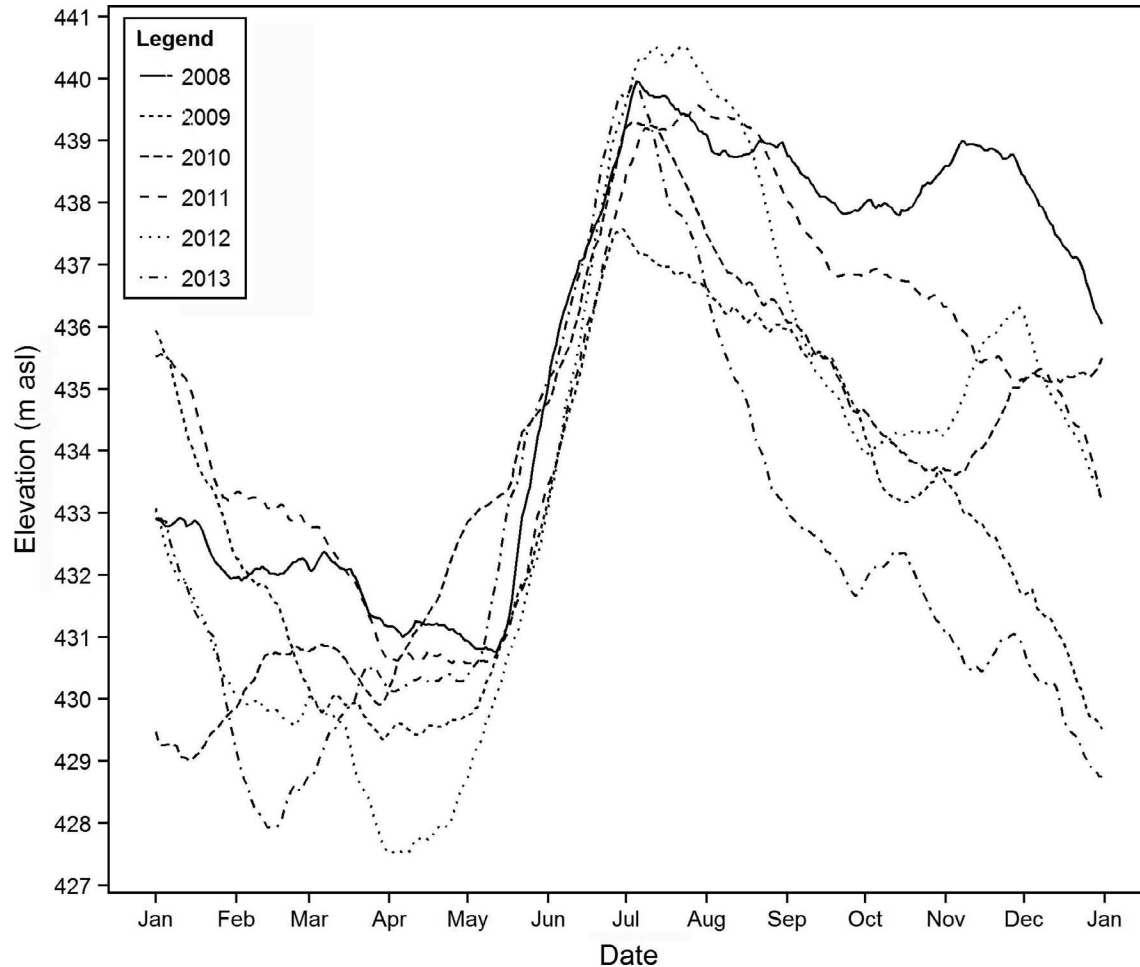
FIGURE 1. Surface water elevations of Arrow Lakes Reservoir, British Columbia, Canada, during our study in 2008–2013 of the impact of reservoir operations on the nesting performance of the Yellow Warbler and the Willow Flycatcher, both of which nest in the reservoir drawdown zone.

habitat flooding affected the daily survival rate (DSR) of their nests. Additionally, flycatchers nested in a unique floating habitat present in the study area, allowing some drawdown zone nests to be protected from nest submergence. Our goal was to provide an objective assessment of how habitat flooding affected nest survival, and to assess whether nesting on a small floating island could mitigate the negative impacts of reservoir operations.

METHODS

Study Area and Field Methods

Our study took place between 2008 and 2013 in the Revelstoke Reach of the Arrow Lakes Reservoir (ALR), which lies within the narrow valley between the Selkirk and Monashee mountains of southeastern British Columbia (BC). Located within the 'interior wet belt' of BC, the region experiences heavy precipitation, primarily during fall and winter, leading to deep snowpack and a pronounced spring freshet. This reservoir is one of many impoundments along the Columbia River; upstream, the river is regulated by 2 other large reservoirs positioned serially head-to-toe. The ALR is controlled at the 52 m high Keenleyside Dam located 230 km downstream, or south of the study area. This embankment dam was completed in 1968 in collaboration with the USA under the Columbia River Treaty. The ALR is primarily operated for storage (capacity $= 8.76$ km^3) to prevent floods and to maximize power production downstream in the USA (BC Hydro 2007). The reservoir is filled annually to near 'full pool' (maximum capacity) during the spring freshet, typically filling during May and June and peaking in early July, the mid-to-late part of the breeding season. The reservoir is typically drawn down in late summer, fall, and winter (Figure 1). ALR water levels fluctuate between 418.6 and 440.1 m asl (BC Hydro 2007). The normal full pool elevation is 440.1 m asl, but the maximum historic elevation was 441.0 m asl, which happened during a

surcharge in 1976. The operations of the reservoir are governed by many factors, including the Columbia River Treaty and Non-Treaty Storage Agreements between Canada and the USA, water use planning 'soft constraints,' and meteorological variation among years (BC Hydro 2007).

Revelstoke Reach, the northern arm of the ALR, represents the upstream head of the reservoir. When not inundated, the Columbia River snakes south through the flat valley bottom floodplain of Revelstoke Reach (all part of the drawdown zone), which supported productive farms prior to impoundment. The floodplain decreases in elevation gradually from north to south and the vegetation community is less complex at the southern (lower) end of the reach. Lenticular sedge (*Carex lenticularis*) is one of the most successful plants to establish at low elevations (above 433 m asl). As the floodplain elevation increases, reed canarygrass (*Phalaris arundinacea*) forms an increasingly dominant ground cover. At or above 436 m asl, willow (*Salix* spp.) and, to a lesser degree, cottonwood (*Populus balsamifera*) become established in a matrix of dense graminoid cover (primarily reed canarygrass). As the floodplain nears full pool elevation ($\sim$439.5–440.1 m asl), a diversity of shrubs and trees are found in areas that closely resemble natural riparian habitat (Quinlan and Green 2012).

We located and followed the fate of warbler and flycatcher nests throughout a 15 km stretch of the ALR drawdown zone at the head of Revelstoke Reach, where shrub growth was well established. Inflowing tributaries (the Illecillewaet River and Drimmie Creek) marked the northern and southern ends of the study area. It was not possible to monitor all available habitat each year, so we monitored subplots within the study area. Three areas (60–80 ha in size) were monitored annually because they encompassed 3 major concentrations of warbler territories (see Quinlan and Green 2012), accounting for 88% of the warbler nest records in this study. There was also 1 site with a minor concentration of flycatchers that was monitored annually ('Montana Slough'; see below). New, smaller monitoring plots were also defined and monitored annually to maximize spatial independence, contributing 12% of warbler nests and 70% of flycatcher nests. These temporary sites typically contributed few nest records each (median = 1 nest from 16 sites for warblers, and 2 nests from 25 sites for flycatchers). For warblers, it was possible that nesting performance varied among sites (e.g., among the 3 major nesting areas) and/or as a function of nesting density. To control for these potential spatial effects in our analysis of the warbler data, we defined a site factor with 4 levels that distinguished between warbler nests from the 3 annually monitored high-density nesting areas and low-density nests scattered throughout the remainder of the study area. Flycatcher nesting was

dispersed more evenly throughout the study area, but there was a minor concentration of flycatchers nesting at Montana Slough, which we monitored for 5 yr of the study due to the unique character of this site. This 4.6 ha site was comprised of sphagnum moss, peat, and an unusually complex diversity of plants, given its relatively low elevation ($\sim$436 m asl). The Montana Slough site floated, becoming an island at high water levels, even when the reservoir was at maximum capacity ($\sim$440 m asl). This floating site provided unique drawdown zone habitat conditions more or less free from nest submergence impacts. In our analysis of the flycatcher data, we distinguished between nests at Montana Slough and nests elsewhere in the drawdown zone.

At each site, nests were located both by observing the activities of adults (e.g., nest building and flights to or from the nest) and through systematic searches of nesting habitat. We recorded the location of each nest using a Garmin GPS (Map76csx; Garmin International, Olathe, Kansas, USA) with a typical accuracy of 3–8 m. Nest-site ground surface elevation was determined using a Digital Elevation Model (DEM; 5 m pixel size). Nest height above the ground was estimated with the aid of a 1.5 m measuring stick, and nest elevation was calculated by adding the nest site's DEM value to the nest's measured height above the ground.

We monitored nests regularly, typically every 3 days, following standard nest monitoring protocols (Martin and Geupel 1993), until the nest had failed or successfully fledged young. We recorded whether there was evidence of nest predation (e.g., pulled nest linings, eggshell fragments, body parts, nest damage, and missing contents) or whether the nest had been submerged. We estimated the date that a clutch was initiated assuming that 1 egg was laid per day, that incubation commenced on the day that the penultimate egg was laid, and that the incubation period lasted 12 days for warblers and 14 days for flycatchers (Lowther et al. 1999, Sedgwick 2000).

Statistical Analysis

Program R was used for all data processing and analysis (R Development Core Team 2006). To compare measured nesting parameters (i.e. spatial or temporal variables), we initially fit a general linear model and assessed the assumptions. Residuals were visually inspected to assess heteroscedasticity among groups. If the assumption of homogeneity of variance was violated, we refit the model using a generalized least squares (GLS) modeling framework (Pinheiro et al. 2012). When assessing timing of nest initiation, we controlled for annual differences using a linear mixed effects (LME) model with year entered as a random intercept. Both the GLS and LME models were fit using functions from the 'nlme' package for R (Pinheiro et al. 2012). We report mean $\pm$ SD unless stated otherwise.

All tests are two-tailed and an alpha level of 0.05 is considered statistically significant.

Nest observation data were formatted for logistic exposure analysis (Shaffer 2004), where the nest's exposure was calculated as the number of days since the previous nest observation, and its survival during the observation period was coded as a binary variable. After nestlings were observed within 2 days of typical fledging age, nest observations were no longer included in the DSR analyses to avoid uncertainties that arose from final nest observations (e.g., whether nestlings died after fledging or while still in the nest). For example, we assumed that warbler nestlings were ready to fledge when 10 days old (Lowther et al. 1999), so once the nestlings were observed at ≥8 days old, no further observations were included in the analysis. For flycatchers, we assumed that nestlings were ready to fledge when 13 days old (Sedgwick 2000). To fit logistic exposure models, we specified a generalized linear model with a binomial distribution and a modified logistic exposure link to accommodate uneven exposure periods in the nest observation data points (Shaffer 2004, Latif et al. 2012). Akaike's Information Criterion corrected for small sample size (AIC_c) was used to select the best supported combination of predictor variables in our models (Burnham and Anderson 2002). Models with a difference in AIC_c value from the top model ($\Delta AIC_c \leq 2$) were considered to have strong support, unless they differed from the best model only by the addition of an 'uninformative parameter' (Arnold 2010).

With the exception of flycatcher nests located on the floating bog habitat at Montana Slough, nest observations were classified as occurring in flooded conditions if the reservoir surface elevation (recorded with a data logger) exceeded the nest site's DEM value during the nest observation period (each period being equal to an ~3-day interval between subsequent nest observations). Thus, there were 2 mutually exclusive options ('not flooded' or 'flooded') indicating the situation during each observation period for warblers; for flycatchers, there were 3 types of nesting condition ('not flooded,' 'flooded,' or 'floating,' the latter for nests located in the floating bog). These options were coded by a factor variable ('habitat condition') that constituted the main effect in our DSR models.

To assess how the habitat condition affected the DSR of warbler and flycatcher nests, we considered several candidate models that allowed us to control for temporal and spatial variation in DSR. We considered 3 temporal covariates. The first was 'nest stage,' a factor with 3 levels: 'laying,' 'incubation,' and 'nestling.' The second was 'year'; the logistic exposure model did not allow the inclusion of random effects, so year was entered as a factor with 6 levels. Finally, 'ordinal date' was a continuous variable indicating how far into the nesting season the observation was made; this was scaled such that day 0 represented the earliest record of when a clutch was initiated. For warblers, we also included 'site' as described above, to control for potential spatial effects.

For warblers, candidate models included the null model (DSR = intercept), and all possible univariate models (5), 2-variable models (10), and 3-variable models (10). It was possible that the impact of reservoir operations depended on the year or site, so multivariate models with interaction terms were also included, with interactions between the main effect and these 2 variables (2 2-variable and 6 3-variable models with interaction terms). A similar approach was used for flycatchers, except that there was no site variable, leading to 4 univariate models, 6 2-variable models, 4 3-variable models, and 2 models with interaction terms.

RESULTS

We monitored 272 warbler nests and 81 flycatcher nests between 2008 and 2013 in the ALR drawdown zone; 24 flycatcher nests were located in the floating bog habitat. Excluding nests located in the floating bog habitat, the median DEM (ground surface) elevations of warbler and flycatcher nests were similar (mean warbler DEM = 438.59 ± 0.84 m asl; mean flycatcher DEM = 438.75 ± 0.94 m asl; minimum elevation = 436.50 m asl for both species). Warblers built their nests higher above the ground (mean warbler nest height = 2.20 ± 1.51 m; mean flycatcher nest height = 1.27 ± 0.63 m; GLS, $F_{1,281} = 50.3$, $P < 0.001$). As a result, the actual nest elevation (DEM + nest height, m asl) of warbler nests was, on average, 0.76 m higher than that of flycatcher nests (GLS, $F_{1,281} = 15.0$, $P = 0.001$), and a larger proportion of warbler nests were positioned above the historic maximum water elevation (Pearson's $\chi^2 = 7.1$, df = 1, $P = 0.008$). The earliest warbler clutch was initiated on May 21, whereas the earliest flycatcher clutch was initiated on June 5. On average, warblers initiated clutches 16.9 days before flycatchers (LME, $F_{1,346} = 200.0$, $P < 0.001$). The differences in nest heights and nesting phenology resulted in considerable partitioning of nesting in time and space (Figure 2).

The proportion of warbler nest observations classified as flooded increased with advancing ordinal date (logistic regression, $P < 0.001$), indicating colinearity between ordinal date and habitat condition. In total, 34% of observations were classified as flooded; observations of flooded habitat generally began on June 15 and became increasingly common thereafter. When habitats were flooded, 28% of nest failures were caused by nest submergence ($n = 16$; Table 1). Nest failures were observed from June 2 through July 22; nest failures caused by submergence generally occurred midway through this time period, with early and late failures primarily caused by other factors such as predation (Figure 3). Seven of the candidate DSR models received strong support ($\Delta AIC_c <$
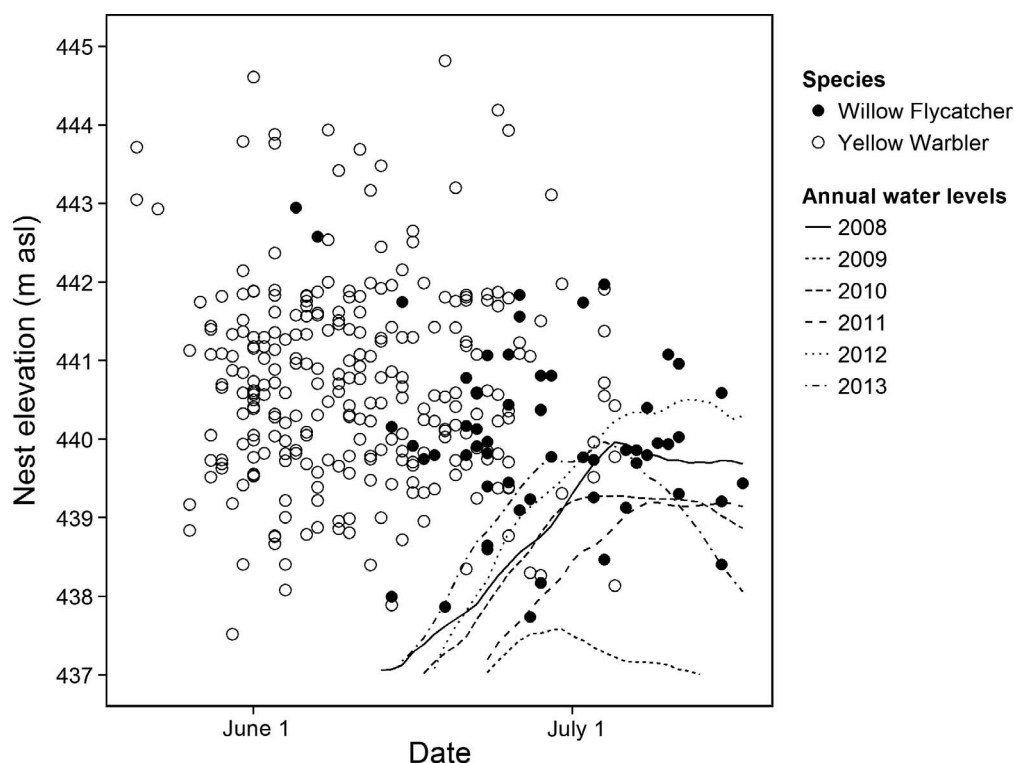
FIGURE 2. Clutch initiation dates and nest elevations for Yellow Warbler and Willow Flycatcher nests located in the drawdown zone of Arrow Lakes Reservoir, British Columbia, Canada. The lines represent observed reservoir water elevations during each year (2008–2013) of the study.

2) and identified ordinal date and habitat condition as important effects; we considered only 3 of these models because the other 4 models contained uninformative variables (Arnold 2010; Table 2). The top model included only the ordinal date term and showed a decline in nest DSR over the breeding season ($P = 0.006$; Figure 4, Table 2). The other 2 considered models each contained habitat condition, but received less than one third of the support given to the ordinal date model (Table 2), with both estimating lower DSR in flooded habitat ('not flooded' DSR $= 0.971 \pm 0.003$; 'flooded' DSR $= 0.956 \pm 0.006$). Considering both the colinearity of ordinal date and habitat condition and the timing of nest submergence, we

accepted the top-ranked ordinal date model as the best model. Removing low-density warbler nests from the analysis (i.e. including only the 3 main nesting areas) did not alter these results.

For flycatchers, 59% of nest observations were classified as flooded, most early in the nesting season. When nesting habitats were flooded, nest submergence due to reservoir operations caused 50% of nest failures (Table 1). Five models had strong support ($\Delta AIC_c < 2$), and all of these contained the habitat condition term. The univariate model had the greatest support and, because the additional variables in the other 4 models were uninformative (Arnold 2010), we accepted this as the best model of nest

TABLE 1. Causes of failure determined for Yellow Warbler and Willow Flycatcher nests under 3 nesting conditions (habitat flooded, habitat not flooded, and nest located on a floating bog island; the latter applies to Willow Flycatcher nests only) in the drawdown zone of the Arrow Lakes Reservoir, British Columbia, Canada, 2008–2013. The number of observation periods indicates how many observations of nest survival were made under each nesting condition.

	Yellow Warbler			Willow Flycatcher			
	Not flooded	Flooded	Total	Not flooded	Flooded	Floating	Total
No. observation periods	855	433	1,288	106	150	161	417
Total no. failures observed	75	58	133	15	20	7	42
No. failures attributed to predation	62	37	99	11	9	4	24
No. failures attributed to submergence	0	16	16	0	10	0	10
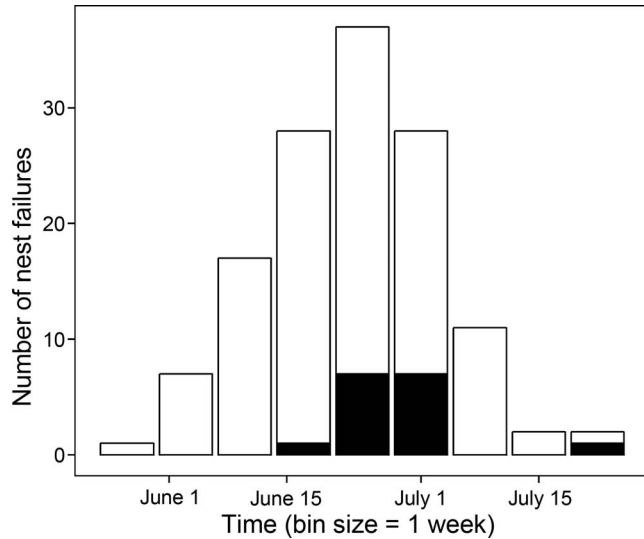
FIGURE 3. Timing of observed Yellow Warbler nest failures in the drawdown zone of Arrow Lakes Reservoir, British Columbia, Canada, 2008–2013. Black bars represent nests that failed due to submergence; white bars represent nests that failed for other reasons (e.g., predation).
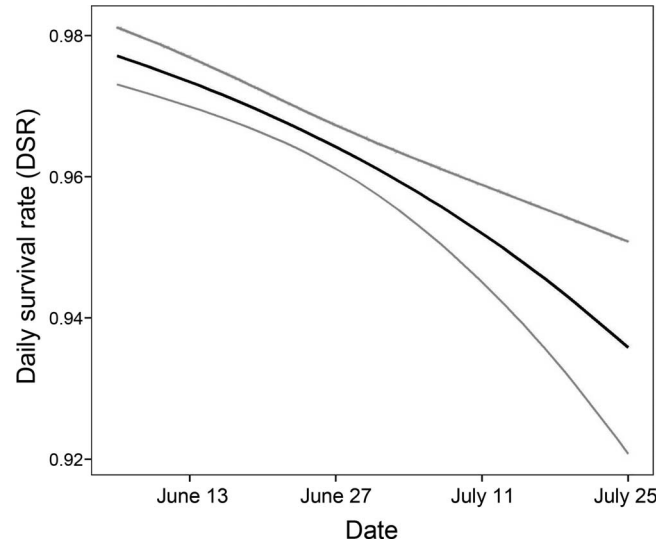
FIGURE 4. The influence of ordinal date on the daily survival rate (DSR) of Yellow Warbler nests located in the drawdown zone of the Arrow Lakes Reservoir, British Columbia, Canada, 2008–2013. Mean DSR $\pm$ SE are plotted.

DSR (Table 3). This model failed to find significant differences in the DSR of nests positioned in flooded habitat (DSR = 0.960 $\pm$ 0.009), compared with those in unflooded situations (DSR = 0.958 $\pm$ 0.012), but there was a significant improvement in DSR for nests positioned on the floating habitat (DSR = 0.986 $\pm$ 0.005, P = 0.02; Figure 5).

DISCUSSION

We assessed whether habitat flooding caused by reservoir operations affected the nest survival of 2 riparian songbird species with differing exposure to nest submergence. Surprisingly, rising water levels that led to nest submergence had little impact on nest DSR for either species. Willow Flycatchers had greater exposure to nest submer-

gence, with 50% of nest failures the direct result of nest submergence when their nesting habitat was flooded; however, their nest DSR was equivalent in both flooded and unflooded conditions. Our results demonstrate that the impact of reservoir operations on breeding birds is more complex for shrub-nesting species than for ground-nesting species (Espie et al. 1998, Anteau et al. 2012), and that the rate of nest submergence per se may be a poor indicator of the impact that reservoir operations have on shrub-nesting species.

The degree to which birds experience nest submergence due to reservoir operations depends on absolute nest elevation and the timing of breeding relative to the operations of the reservoir. Nest elevation, in turn, depends on the distribution of nesting habitat and nest height above the ground. As such, there is a continuum in the exposure

TABLE 2. Comparison of support for models of Yellow Warbler daily nest survivorship in the drawdown zone of the Arrow Lakes Reservoir, British Columbia, Canada, 2008–2013. Models were ranked based on the difference from the top model in Akaike's Information Criterion corrected for small sample size (ΔAIC$_c$). K is the number of model parameters, Dev is the deviance, and w_i is the Akaike weight. Only models that were well supported (ΔAIC$_c$ < 2) are presented.

Model	K	Dev	ΔAIC$_c$ [‡]	w_i
Ordinal date	2	854.1	0.00	0.17
Ordinal date + Nest stage [†]	4	850.4	0.33	0.14
Ordinal date + Habitat condition [†]	3	853.2	1.18	0.09
Ordinal date + Nest stage + Habitat condition [†]	5	849.5	1.51	0.08
Habitat condition + Site	5	849.8	1.77	0.07
Ordinal date + Habitat condition + Site [†]	6	847.9	1.84	0.07
Habitat condition	2	855.9	1.85	0.07

[‡] The minimum AIC$_c$ = 858.1.
[†] Rejected model due to inclusion of uninformative variables.

TABLE 3. Comparison of support for the models of Willow Flycatcher daily nest survivorship in the drawdown zone of the Arrow Lakes Reservoir, British Columbia, Canada, 2008–2013. Models were ranked based on the difference from the top model in Akaike's Information Criterion corrected for small sample size (ΔAIC_c). K is the number of model parameters, Dev is the deviance, and w_i is the Akaike weight. Only models that were well supported ($\Delta AIC_c < 2$) are presented.

| Model	K	Dev	ΔAIC_c [‡]	w_i
Habitat condition	3	251.9	0.00	0.23
Habitat condition + Ordinal date + Nest stage [†]	6	251.5	0.79	0.16
Habitat condition + Nest stage [†]	5	248.7	0.82	0.15
Habitat condition + Year [†]	4	251.6	1.69	0.10
Habitat condition + Ordinal date [†]	4	251.8	1.90	0.09

[‡] The minimum $AIC_c = 258.0$.
[†] Rejected model due to inclusion of uninformative variables.

of shrub-nesting species to nest submergence. In our study, the observed proportion of nest failures caused by nest submergence was almost double for flycatchers compared with warblers, because flycatchers positioned their nests lower in shrubs and nested later in the year. Flycatchers were likely at the extreme end of the continuum among species nesting at the ALR, with a relatively high exposure to nest submergence compared with other shrub-nesting species. Yellow Warblers had moderate exposure to nest submergence. Other species (e.g., American Redstart [*Setophaga ruticilla*]) nest higher above the ground and restrict nesting to within the top 1–2 m of the drawdown zone, and would therefore have even lower exposure to nest submergence in the ALR. While the exposure of each species to nest submergence by reservoir operations may be predictable, our results indicate that the level of exposure and subsequent nest failure due to nest submergence do not necessarily correlate with overall nesting success for shrub-nesting species.

Because flooding of drawdown zone habitat, which caused nest failure, did not affect the DSR of warbler and flycatcher nests, other causes of nest failure were likely reduced by habitat flooding. Predation is a major cause of nest failure in many songbirds (Martin 1995), and several studies have shown that predation rates are reduced if birds nest over water (Picman et al. 1993, Cain et al. 2003, Hoover 2006, Roy Nielsen and Gates 2007, Robertson and Olsen 2015). We suspect that reduced predation pressure associated with habitat flooding may have contributed to our results, especially for flycatchers for which there were relatively fewer predation events in flooded habitat. Further work, however, is required to confirm that nest predation rates are influenced by reservoir water levels.

It has been unclear whether shrub growth persisting in reservoir drawdown zones compensates for riparian habitat loss, or whether drawdown zone vegetation negates conservation benefits by creating an ecological trap. Drawdown zone habitat may function as an ecological trap for shrub-nesting birds because rising water levels may submerge nests or indirectly reduce nest success.

However, we found little evidence that the inundation of drawdown zone habitat reduced nest success for warblers or flycatchers. Drawdown zone habitat might also function as an ecological trap because the modified habitat appears suitable but is less productive than habitat elsewhere. We did not measure the DSR of warbler and flycatcher nests outside the drawdown zone, but the DSR values that we recorded are similar to previously reported nest DSR for Yellow Warblers (0.94–0.99; Tewksbury et al. 1998, Willson and Gende 2000, Galigan et al. 2006, Richardson et al. 2009, Latif et al. 2012) and for Willow Flycatchers (0.78–0.98; Galigan et al. 2006, Stumpf et al. 2012). This suggests that drawdown zone habitat within the ALR does not
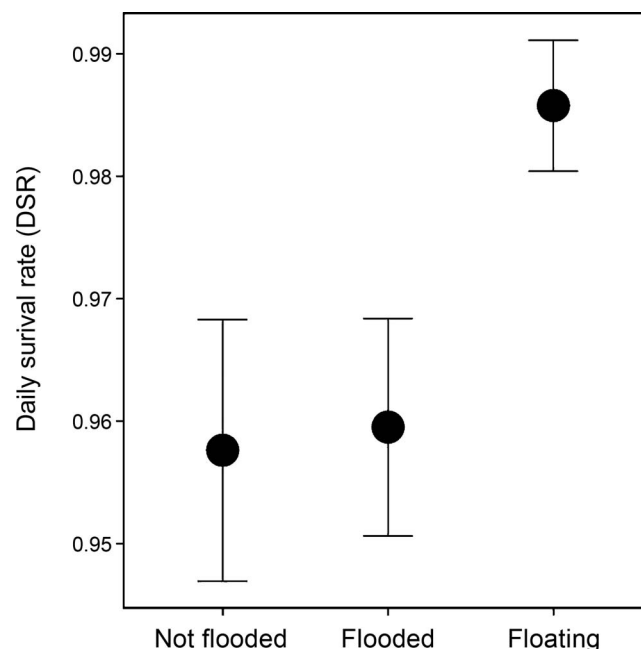
FIGURE 5. Daily survival rates (DSR) calculated for Willow Flycatcher nests located in the drawdown zone of the Arrow Lakes Reservoir, British Columbia, Canada, 2008–2013. Despite suffering considerable apparent costs of nest submergence in flooded habitat, DSR was unaffected, but was enhanced for nests located on a floating island. Mean DSR ± SE are plotted.

function as an ecological trap, corroborating previous work from the ALR on Yellow Warblers by Quinlan and Green (2012). We note, however, that our study and previous work (Quinlan and Green 2012) examined the impact of reservoir operations on nest success and/or the number of fledglings produced. Drawdown zone habitat could still function as an ecological trap if flooding of nesting habitat influences postfledging survival. Nest survival in flooded environments will be less relevant to overall productivity if fledglings are highly vulnerable to drowning.

While our study clearly suggests that the impact of reservoir operations on shrub-nesting birds cannot be assessed by simply observing occurrences of nest submergence, not all species fare well in reservoir drawdown zones (e.g., Anteau et al. 2012), and many populations have suffered habitat loss following reservoir creation. There is increasing interest in compensating for the negative impacts caused by reservoirs. Our study showed that nesting on floating substrates can be beneficial; flycatchers nesting on a naturally floating bog habitat had higher DSR than flycatchers elsewhere in the ALR. Predation rates on the floating bog habitat were low for the Willow Flycatcher nests in our study, and may have been low for other shrub-nesting species and possibly ground-nesting birds as well. It is possible that creating floating islands could be a potential mitigation measure for some nesting species. This may seem unfeasible in practical terms, but a similar method has previously been effective for Caspian Terns (*Hydroprogne caspia*; Collis et al. 2002), and the approach should be investigated further.

This study provides the first assessment of how habitat flooding affects nest survivorship of shrub-nesting birds in reservoir drawdown zones. The results suggest that habitat flooding has surprisingly little impact on nest DSR, and that shrub growth in reservoir drawdown zones does not necessarily present an ecological trap, despite nests frequently becoming submerged. Because the ALR has unusually well-developed drawdown zone vegetation and a high potential for submerging nests, we suggest that our study represents an extreme example of how nest submergence may affect shrub-nesting bird species. Future studies should examine how postfledging juvenile survivorship is affected by habitat flooding in the ALR and in other reservoirs where nest submergence is an issue, to fully determine the value of reservoir drawdown zone shrub as breeding habitat in these environments.

ACKNOWLEDGMENTS

We thank Doug Adama and Ed Hill who were instrumental in the early years of this project. We are grateful to Margo Dennis, Susan Pinkus, and Jason Watson from BC Hydro for assisting us with this study. We are indebted to Christine Rock

LITERATURE CITED

Anteau, M. J., T. L. Shaffer, M. H. Sherfy, M. A. Sovada, J. H. Stucker, and M. T. Wiltermuth (2012). Nest survival of Piping Plovers at a dynamic reservoir indicates an ecological trap for a threatened population. Oecologia 170:1167–1179.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Baschuk, M. S., N. Koper, D. A. Wrubleski, and G. Goldsborough (2012). Effects of water depth, cover and food resources on habitat use of marsh birds and waterfowl in boreal wetlands of Manitoba, Canada. Waterbirds 35:44–55.

Baxter, R. M. (1977). Environmental effects of dams and impoundments. Annual Review of Ecology and Systematics 8:255–283.

BC Hydro (2007). Columbia River Project Water Use Plan. http://www.bchydro.com/about/sustainability/conservation/water_use_planning/southern_interior/columbia_river.html

Berga, L., J. M. Buil, E. Bofill, J. C. De Cea, J. A. Garcia Perez, G. Mañueco, J. Polimon, A. Soriano, and J. Yagüe (Editors) (2006). Dams and Reservoirs, Societies and Environment in the 21st Century. Proceedings of the International Symposium on Dams in Societies of the 21st Century; 18 June 2006; Barcelona, Spain. Taylor and Francis Group, London.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York.

Cain, J. W., III, M. L. Morrison, and H. L. Bombay (2003). Predator activity and nest success of Willow Flycatchers and Yellow Warblers. Journal of Wildlife Management 67:600–610.

Calvert, A. M., C. A. Bishop, R. D. Elliot, E. A. Krebs, T. M. Kydd, C. S. Machtans, and G. J. Robertson (2013). A synthesis of human-related avian mortality in Canada. Avian Conservation and Ecology 8(2):11. http://dx.doi.org/10.5751/ACE-00581-080211

Cocimano, M. C., M. L. Morrison, H. A. Mathewson, and L. M. Vormwald (2011). The influence of meadow moisture levels on activity of small mammal nest predators in the Sierra Nevada, California. Northwestern Naturalist 92:50–56.

Collis, K., D. D. Roby, C. W. Thompson, D. E. Lyons, and M. Tirhi (2002). Barges as temporary breeding sites for Caspian Terns: Assessing potential sites for colony restoration. Wildlife Society Bulletin 30:1140–1149.

Desgranges, J.-L., J. Ingram, B. Drolet, J. Morin, C. Savage, and D. Borcard (2006). Modelling wetland bird response to water level changes in the Lake Ontario–St. Lawrence River hydrosystem. Environmental Monitoring and Assessment 113:329–365.

Ellis, L. A., S. D. Stump, and D. M. Weddle (2009). Southwestern Willow Flycatcher population and habitat response to reservoir inundation. Journal of Wildlife Management 73:946–954.

Espie, R. H. M., P. C. James, and R. M. Brigham (1998). The effects of flooding on Piping Plover *Charadrius melodus* reproductive success at Lake Diefenbaker, Saskatchewan, Canada. Biological Conservation 86:215–222.

Galigan, E. W., T. L. DeVault, and S. L. Lima (2006). Nesting success of grassland and savanna birds on reclaimed surface coal mines of the midwestern United States. Wilson Journal of Ornithology 118:537–546.

Hatten, J. R., E. H. Paxton, and M. K. Sogge (2010). Modeling the dynamic habitat and breeding population of Southwestern Willow Flycatcher. Ecological Modeling 221:1674–1686.

Hoover, J. P. (2006). Water depth influences nest predation for a wetland-dependent bird in fragmented bottomland forests. Biological Conservation 127:37–45.

Latif, Q. S., S. K. Heath, and G. Ballard (2012). The nest predator assemblage for songbirds in Mono Lake Basin riparian habitats. Western North American Naturalist 72:276–287.

Lehner, B., C. Reidy Liermann, C. Revenga, C. Vörösmarty, B. Fekete, P. Crouzet, P. Döll, M. Endejan, K. Frenken, J. Magome, C. Nilsson, et al. (2011). High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. Frontiers in Ecology and the Environment 9: 494–502. http://dx.doi.org/10.1890/100125

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector (1999). Yellow Warbler (*Dendroica petechia*). In The Birds of North America Online (A. Poole, Editor), Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/454 doi:10.2173/bna.454

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101–127.

Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

Nilsson, C., and M. Dynesius (1994). Ecological effects of river regulation on mammals and birds: A review. Regulated Rivers: Research & Management 9:45–53.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga (2005). Fragmentation and flow regulation of the world's large river systems. Science 308:405–408.

Parsons, K. C. (2002). Integrated management of waterbird habitats at impounded wetlands in Delaware Bay, U.S.A. Waterbirds 25(Special Publication 2):25–41.

Picman, J., M. L. Milks, and M. Leptich (1993). Patterns of predation on passerine nests in marshes: Effects of water depth and distance from edge. The Auk 110:89–94.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team (2012). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103. http://CRAN.R-project.org/package=nlme

Quinlan, S. P., and D. J. Green (2012). Riparian habitat disturbed by reservoir management does not function as an ecological trap for the Yellow Warbler (*Setophaga petechia*). Canadian Journal of Zoology 90:320–328.

Rains, M. C., J. F. Mount, and E. W. Larsen (2004). Simulated changes in shallow groundwater and vegetation distributions under different reservoir operations scenarios. Ecological Applications 14:192–207.

R Development Core Team (2006). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. www.R-project.org

Richardson, T. W., T. Gardali, and S. H. Jenkins (2009). Review and meta-analysis of camera effects on avian nest success. Journal of Wildlife Management 73:287–293.

Robertson, B. A., and R. L. Hutto (2006). A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.

Robertson, E. P., and B. J. Olsen (2015). Behavioral plasticity in nest building increases fecundity in marsh birds. The Auk: Ornithological Advances 132:37–45.

Roy Nielsen, C. L., and R. J. Gates (2007). Reduced nest predation of cavity-nesting Wood Ducks during flooding in bottomland hardwood forest. The Condor 109:210–215.

Rundle, W. D., and L. H. Fredrickson (1981). Managing seasonally flooded impoundments for migrant rails and shorebirds. Wildlife Society Bulletin 9:80–87.

Sedgwick, J. A. (2000). Willow Flycatcher (*Empidonax traillii*). In The Birds of North America Online (A. Poole, Editor), Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/533 doi:10.2173/bna.533

Shaffer, T. L. (2004). A unified approach to analyzing nest success. The Auk 121:526–540.

Stumpf, K. J., T. C. Theimer, M. A. Mcleod, and T. J. Koronkiewicz (2012). Distance from riparian edge reduces brood parasitism of Southwestern Willow Flycatchers, whereas parasitism increases nest predation risk. Journal of Wildlife Management 76:269–277.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin (1998). Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890–2903.

Willson, M. F., and S. M. Gende (2000). Nesting success of forest birds in southeast Alaska and adjacent Canada. The Condor 102:314–325.

Wiltermuth, M. T., M. J. Anteau, M. H. Sherfy, and T. L. Shaffer (2009). Nest movement by Piping Plovers in response to changing habitat conditions. The Condor 111:550–555.

Wolf, K. (1955). Some effects of fluctuating and falling water levels on waterfowl production. Journal of Wildlife Management 19:13–23.