Post-fledging survival and habitat use of juvenile Least Bitterns (*Ixobrychus exilis*)

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ABSTRACT—The post-fledging period, defined as the period after a young bird leaves its nest, is a crucial stage for birds and is often when they face the highest risk of mortality. Current management for breeding birds has been primarily informed by the nesting and adult stages while the post-fledging period is often understudied, despite birds spending an equal or greater amount of time in the post-fledging period than they do in the nest. In 2020 and 2021 we documented habitat used, including water depth and vegetation height, cover, and type, and survival of 50 fledglings of Least Bittern (*Ixobrychus exilis*), a cryptic marsh bird of conservation concern in the midwestern United States. We compared habitat used by fledglings to habitat at randomly selected points within a daily dispersal distance determined by the fledgling's age. Fledglings used points with denser and taller marsh vegetation than random points and they relied on persistent emergent vegetation, which likely provides greater predator protection, thermal refuge, and foraging opportunities. Fledgling habitat use was age-dependent and related to flight ability, with younger, pre-flight fledglings using denser habitats and older juveniles with flight ability using more open habitat. Additionally, 86% of Least Bittern fledglings survived until 30 d post-hatch (when they often left the marsh they hatched in), a higher survival rate than in the limited previous studies of fledglings. Mortality resulted from predation and exposure, and the greatest mortality risk was in the 3 d following fledging and in 2020. Our results suggest that managing for a diversity of marsh habitats, including both densely vegetated habitats commonly used by nesting Least Bitterns and more open marsh habitats, is important for fledglings. *Received 18 November 2023. Accepted 8 August 2024.*

Key words: habitat selection, *Ixobrychus exilis*, Least Bittern, mortality, post-fledging, wetland management.

Sobrevivencia post-emancipación y uso de hábitat de juveniles de avetorrillo *Ixobrychus exilis*

RESUMEN (Spanish)—El periodo post-emancipación, definido como el período de vida de la joven ave posterior a la partida del nido, es una etapa crucial para las aves y es usualmente cuando enfrentan el mayor riesgo de mortalidad. El manejo actual de reproducción de aves ha sido principalmente informado por los estadíos de anidamiento y adultez mientras que la etapa post-emancipación es a menudo poco estudiada, aunque las aves duren igual o más tiempo en la etapa de post-emancipación que en el nido. En 2020 y 2021 documentamos el hábitat usado, incluyendo profundidad de agua y altura de vegetación, cobertura y tipo, así como sobrevivencia de 50 volantones de avetorrillo *Ixobrychus exilis*, un ave críptica de pantano con preocupación de conservación en el medioeste de Estados Unidos. Comparamos el uso de hábitat de volantones en puntos seleccionados al azar dentro de una distancia de dispersión diaria determinada por la edad del volantón. Los volantones usaron puntos con vegetación más densa y más alta que la de los puntos al azar y dependieron de vegetación persistente emergente, que posiblemente proporciona mayor protección contra depredadores y se relaciona a la habilidad de vuelo, así como oportunidades de forrajeo. El uso de hábitat por los volantones dependía de su edad y se relacionaba con la habilidad de vuelo, con jóvenes volantones pre-vuelo que usaban más densos y juveniles mayores con habilidad de vuelo que usaban hábitat más abierto. Adicionalmente, 86% de los volantones de avetorrillo *Ixobrychus exilis* sobrevivieron hasta el día 30 post eclosión (cuando por lo general abandonaron el pantano en el que eclosionaron), lo que representa una tasa mayor de sobrevivencia que en los limitados estudios previos acerca de volantones. La mortalidad fue el resultado de depredación y exposición y el mayor riesgo de mortalidad se presentaba en los 3 días posteriores a la emancipación y en 2020. Nuestros resultados sugieren que el manejo para la diversidad de los hábitats de pantano, incluyendo tanto hábitats de vegetación densa, comúnmente usada por avetorrillos *Ixobrychus exilis* que anidan y hábitats pantanosos más abiertos, es importante para los volantones.

Palabras clave: avetorrillo, *Ixobrychus exilis*, manejo de humedal, mortalidad, post-emancipación, selección de hábitat.

Studies of habitat use during the breeding season tend to focus on the nesting period, ignoring the months before and after nesting, and their results are often used to inform management of habitat for the entire breeding season. The post-fledging period, the time between when a bird leaves the nest and reaches independence, is a critical and challenging life history stage across all bird species, but it remains relatively understudied and the few studies of altricial or semi-altricial fledglings are restricted to songbirds (Small et al. 2015, Naef-Daenzer and Grüebler 2016, Jones et al. 2017). Fledglings are non-territorial and cryptic, making traditional resighting and recapturing methods ineffective. The cryptic nature of fledglings has likely contributed to the limited studies of this life stage, but the increased use of radio-telemetry has helped to mitigate these challenges (Bogner and

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Baldassarre 2002, White and Faaborg 2008, Raybuck et al. 2020). Studies have demonstrated that habitat needs during the post-fledging period often differ from what adult birds require, as seen in studies of forest birds (Anders et al. 1998, Burke et al. 2017, Raybuck et al. 2020), waterbirds (Morton et al. 1989), and grassland birds (Small et al. 2015). Furthermore, the post-fledging period is dynamic, and as fledglings learn new skills and gain independence, age-specific patterns of habitat use can arise and further complicate management decisions (White and Faaborg 2008, Jones et al. 2017). These patterns may be a result of changes in mobility: older fledglings can fly and can therefore prioritize resource acquisition over strict predator protection and select riskier habitats less conducive to predator avoidance (Small et al. 2015, Raybuck et al. 2020).

The post-fledging period is also of critical importance for population persistence because survival is often lower in this stage than others due to fledglings' inexperience foraging, navigating, and avoiding predators (Anders et al. 1997, Parker et al. 2003, Cox et al. 2014). Furthermore, survival may vary with juvenile age, as increased mobility and flight ability likely allow for greater predator evasion (Anders et al. 1997, Raybuck et al. 2020), while vegetation structure and presence of water may provide enhanced protection and concealment for younger birds with less mobility (Anders et al. 1998, Bogner and Baldassarre 2002, Jones and Bock 2005, Jones et al. 2017). For management and conservation actions to be effective, decisions should be informed by all life stages, including the post-fledging period, but we lack information on this period for most species (Norris and Marra 2007, Cox et al. 2014).

The Least Bittern (*Ixobrychus exilis*) is an inconspicuous wetland-obligate bird and, like many marsh birds, has experienced widespread population declines, primarily driven by habitat loss and degradation (Eddleman et al. 1988, Ward et al. 2010). In the upper midwestern United States, the Least Bittern has undergone a 4.9% annual decline, although estimates are likely inaccurate because secretive wetland birds tend to be poorly sampled in classic roadside surveying efforts (Kleen et al. 2004, Lawler and O'Connor 2004, Gray et al. 2013). In the United States, 53% of wetland area recorded prior to the 1780s was

drained by the 1980s for agricultural expansion and urbanization, and the midwestern United States was particularly impacted by this drainage effort (Dahl 1990). In more recent decades, wetlands are being restored and managed to support a wide suite of wetland-dependent species. One management strategy used in emergent wetlands is periodically dewatering wetlands to mimic historical flood regimes, recharge groundwater, control the spread of invasive species (i.e., *Phalaris arundinacea*; Lavergne and Molofsky 2006), and restore habitat structure and complexity for a variety of wetland plants and animals (i.e., moist-soil plants, waterfowl, shorebirds, marsh birds; Lane and Jensen 1999, USEPA 2008, Guhin and Hayes 2015). Water-level management creates a mosaic of vegetation cover types, including emergent hemi-marsh (i.e., 50:50 water:vegetation) and non-persistent emergent, open water, and mudflat, benefitting diverse plant and animal communities, including many species of marsh birds (Rundle and Fredrickson 1981, Wilson 2016, Tozer et al. 2018, Fournier et al. 2019).

In Least Bitterns, adult occupancy has been found to be greatest in hemi-marsh conditions, described as areas of high degrees of vegetation interspersion, and inundation of 0–57 cm, and adult habitat use is generally used to inform habitat management for the species (Bogner and Baldassarre 2002, Rehm and Baldassarre 2007, Bolenbaugh et al. 2011, Bradshaw et al. 2020). Juvenile Least Bitterns may benefit from this management in their early stages of development because they use their nest for 12–18 d post-hatch (Bogner and Baldassarre 2002, Poole et al. 2020), although with decreasing frequency after 5 d post-hatch, and continue to use the area surrounding the nest for an additional 1–2 weeks (Nero 1950). During this time, it is assumed they are being provisioned equally by their parents through regurgitation; however, very limited information exists to support or refute this idea, in part because adults and fledglings are cryptic (Nero 1950, Poole et al. 2020). Approximately 30 d post-hatch, fledgling Least Bitterns may separate from their parents, which also coincides with the age when fledglings attain flight (29 d; Bogner and Baldassarre 2002). Due to the limited information that exists about Least Bittern fledging

behavior, especially after they separate from their parents, there is a need to understand habitat use and survival to better inform habitat management. This study aims to determine habitat use and causes of mortality in Least Bittern fledglings after leaving the nest. More specifically, we studied habitat use and survival in Least Bittern fledglings as a function of age, habitat conditions, and temporal factors. We expected to see age-specific patterns of habitat use and survival and high mortality due to predation, starvation, or exposure in the post-fledging period.

Methods

Study system

We studied Least Bittern post-fledging survival and habitat use in 2020 and 2021 at Emiquon Preserve (40.35266, −90.08712), a 2,723 ha floodplain wetland in Fulton County, Illinois, USA, managed by The Nature Conservancy (Chen et al. 2017). The backwater lakes of Emiquon Preserve once supported the most productive floodplain ecosystem in Illinois (Chen and Lemke 2009, vanMiddlesworth et al. 2015); however, in 1924, following levee construction, what is now Emiquon Preserve was disconnected from the Illinois River, drained, and used for agriculture for 80 years (Havera et al. 2003, Lemke et al. 2017). In 2000, The Nature Conservancy purchased the land to restore the floodplain wetland and its ecosystem services, and presently uses 2 electrically powered 32,000 gallon per minute (gpm) pumps to mimic natural flood pulses and seasonally dewater the wetland. Today, Emiquon Preserve provides habitat for hundreds of thousands of waterfowl and other waterbirds during migration and provides breeding habitat for marsh birds, including Least Bitterns, within its complex shoreline (Fournier et al. 2021, Schmidt et al. 2023). Least Bitterns are a migratory species and arrive in Illinois in April and nest May through July before departing in September (Illinois DNR 2021).

Capturing and marking fledglings

From May through July 2020 and 2021, we located Least Bittern nests by systematically surveying dense emergent vegetation and hemi-marsh (Schmidt et al. 2023). We visited 50 nests throughout the study period every 3–5 d until nestlings reached fledging age (day 12–18 post-hatch; Bogner and Baldassarre 2002). At these visits, we recorded fledgling mass ($n = 342$; Supplemental Fig. S1), and at 15 d post-hatch fledglings weighed between 56 and 85 g (mean 68 g). From a subset of nests (1–2 per brood) aged 15 d post-hatch, we superglued a 1.7 or 3.0 g VHF radio-tag (<5% body mass; Raim 1978) with a 64 or 185 day life expectancy, respectively (Lotek, Newmarket, Ontario, Canada) between each fledgling's scapulars with the antenna pointing toward the tail (Raim 1978). Fledglings were also banded with a USGS aluminum band and a unique combination of plastic color bands on their tarsometatarsus.

Radio telemetry

We located fledglings once every 1–6 d (mean = 2.53 d; 72.76% of observations recorded every 3 d) between 0530 h and 1600 h (CDT) when they were expected to be active. We located fledglings using homing techniques with a receiver (Advanced Telemetry Systems, Isanti, Minnesota, USA) and a 3-element Yagi antenna from 17 June to 21 August in 2020 and 4 July to 8 August in 2021. We did not track fledglings in adverse weather (i.e., high winds, heavy rain, lightning), which caused some variation in our observation intervals and timing of fledgling detections across the day. Additionally, fledglings often occupied dense or difficult to navigate habitat, and as they were identified serially, we could not locate fledglings at evenly spaced time intervals. Before fledglings attained flight (day 15–29 post-hatch; Bogner and Baldassarre 2002), they would generally remain motionless in a bill-up stance or move quickly through vegetation by grasping stems with their feet, allowing us to determine exact fledgling locations. After fledglings attained flight (≥29 d post-hatch; Bogner and Baldassarre 2002), the birds would often take flight when we approached, and color bands were visible in flight. We determined fledgling location based on these visual encounters or when the signal strength indicated the bird was present but had moved before we visually located it. All locations were recorded on a handheld GPS device (Garmin, Olathe, Kansas, USA). From our 2020 data, when birds were tracked daily, we calculated the minimum daily distance moved by calculating

the Euclidean distance between a fledgling's GPS location and the previous day's location. We stopped tracking fledglings if the radio-tag fell off, the fledgling died, the fledgling left our site, or the date was 21 August 2020 or 8 August 2021, when all tagged birds were >26 d old, an age after which tags were frequently dropped or birds left the site.

Vegetation measurements

We documented habitat characteristics at fledgling locations and at paired random points in 2021. Habitat measurements were taken the same day a fledgling was resighted at both the fledgling location ("used" habitat point) and the paired random point (an available location that the fledgling could have selected). The random point was selected using a random cardinal direction (1–4, north = 1) and distance from the fledgling location. Distance from the fledgling location was age-specific based on movement data from 2020. Paired points were between 0 and 25 m for fledglings 15–20 d post-hatch, 26–100 m for 21–28 d post-hatch, and 101–250 m for ≥29 d post-hatch (Supplemental Fig. S2). If the random point was not in usable habitat for Least Bitterns (i.e., deep open water without perching material), we reselected a random distance and direction.

We recorded water depth, height of emergent vegetation (mean height of shortest and tallest vegetation from root to tip within 1 m of the located fledgling), and percent cover of water and emergent vegetation within 2.5 m at each fledgling location and paired random point using measuring tape. Within the same radius, we also classified each point into 1 of 3 dominant vegetation types: persistent emergent (*Typha* spp. and *Scirpus* spp.), floating leaved (*Nelumbo* spp.), or other (mudflat, non–persistent emergent, woody), as well as 1 of 3 categories for habitat openness: open marsh (open water or aquatic bed interspersed with 0–30% cover by emergent vegetation), hemi-marsh (open water or aquatic bed interspersed with 40–60% cover by emergent vegetation), or dense marsh (open water or aquatic bed interspersed with 70–100% cover by emergent vegetation). If a fledgling could not be located and we assumed the bird was in motion or out of range, habitat measurements were not

taken. We also measured distance to the nest for located fledglings using the coordinates of the nest and fledgling and the measure tool in ArcGIS (ESRI, Redlands, California, USA).

Fledgling fate

Fledglings were assigned 1 of 3 fates during each tracking event: (1) survived = seen alive or radiotracking indicated they were moving after the signal became weaker when the tracker reached the location of the fledgling but could not visually locate them given their cryptic behaviors before they dispersed; (2) died = found dead or limbs were found with key identifiers (i.e., leg bands, radio-tag); or (3) unknown = radio-tag was found not attached to the bird and fate was unknown, or the VHF signal was out of range. If a bird with an unknown fate was subsequently found alive, we retroactively classified the fledgling's fate as survived for the previous unknown interval.

Statistical analyses

We examined daily mass of nestlings and fledglings up to 3 d post-fledging using a linear regression with the *lm* function in R after confirming assumptions were met (R Core Team 2013). Next, we examined daily distance traveled by age to inform the selection radius of paired random points for our habitat-use analyses. We log-transformed distance to meet normality assumptions and fit a linear regression using the g*lmer* function and a Gaussian distribution in the *lme4* package in R (R Core Team 2013, Bates et al. 2015). We included bird ID and nest ID as random effects to account for the nonindependence of sampling the same individual multiple times and sampling more than one individual from the same nest, citing the risk of birds in the same clutch occupying similar spaces when they have limited mobility (Anders et al. 1998).

To examine habitat differences between used and random points we used a generalized linear mixed model with the *glmer* function and a binomial distribution and logit link function in the *lme4* package in R (R Core Team 2013, Bates et al. 2015). We included bird ID, nest ID, and a unique identifier for paired points as random effects to account for the nonindependence of sampling the same individual multiple times,

sampling more than one individual from the same nest, and having pairs of used and random locations. Our response variable was whether a point was used (1) or randomly selected (0), and our predictor variables were water depth, emergent vegetation height, and category of habitat openness. We measured the correlation of variables within models to ensure highly correlated variables ($|r| > 0.7$) were not used in models together, and we tested all models for overdispersion. We ranked models using an information-theoretic approach corrected for small sample sizes (AICc; Burnham and Anderson 2002) and considered models within 8 ΔAICc units of the top model to be competitive. We calculated probability of use for variables in competitive models using the least-square means function in the *emmeans* package in R (R Core Team 2013). Models with dominant vegetation had convergence problems identified as quasi-complete separation (Supplemental Table S1) and the variable was excluded from these analyses and run separately as a bias-reduced logistic regression, Firth correction in the *logistf* package, and presented as coefficient estimates (β) and 95% confidence intervals (Firth 1993, R Core Team 2013, Bates et al. 2015). We also examined habitat use versus availability for fledglings pre-flight and post-flight in 2 separate analyses using the same methods above. Flight was attained between 23 and 38 d of age (mean = 31 d), so we used a cutoff of 31 d to determine flight ability for habitat use.

To examine post-fledging survival as a function of habitat variables, we developed a priori hypotheses containing variables believed to impact fledgling survival, tested coefficients to meet model assumptions, and ran logistic exposure models (Shaffer 2004). While typically used to analyze nest survival, logistic exposure has been applied to studies of fledgling survival and predation risk in a range of species including Ovenbirds (*Seiurus aurocapilla*), Acadian Flycatchers (*Empidonax virescens*), and Golden-winged Warblers (*Vermivora chrysoptera*) (Streby et al. 2013, Jenkins et al. 2016). Our response variable was fledgling fate (survived or died) for each interval, and intervals that ended with an unknown fate (i.e., signal out of range) were not included in the analysis because fate could not be

knowingly attributed to a predation event or the individual flying out of range. Our predictor variables were water depth, year, day of the year, age, and dominant vegetation and habitat openness categories. We assessed correlation among variables within models to ensure highly correlated variables ($|r| > 0.7$) were not used in models together and examined models for overdispersion. We again ranked models using AICc (Burnham and Anderson 2002). We considered these models to be competitive when within 2 ΔAICc units of the most parsimonious model, rather than 8 ΔAICc units as used above, because here we did not have random effects providing additional parameters. We reported our results as daily survival rates, calculated using the *lsmeans* function in the *emmeans* package in R, the estimate of which was input into an odds ratio for a 2 week period of time (R Core Team 2013).

Results

Fledgling radio-tagging

Fledging dates ranged from 15 June to 14 August in 2020 and from 30 June to 12 August in 2021. We attached transmitters to 50 fledglings (2020 = 16, 2021 = 34) and determined their fate and location every 1–4 d (mean = 2.5 d). Tag retention averaged 15.4 d (range = 0–29 d). Fledglings attained flight around day 31 post-hatch (± 3.8 [SD]; range = 23–37 d) and juvenile movement increased with age, and subsequently flight ability (Supplemental Fig. S2). Fledglings that dropped their tag or were not spotted after the first interval were not included in analyses of survival or habitat use. In total, we monitored 44 Least Bittern fledglings from 29 nests (mean = 1.5 fledglings/nest, range = 1–2).

Fledgling habitat use

We measured habitat characteristics at 231 fledgling locations and 231 paired points for 34 Least Bittern fledglings in 2021. The best-supported model included the additive effects of habitat openness and emergent vegetation height ($w_i = 1.00$; Table 1, Table 2). Probability of being a used point increased in taller emergent vegetation and there was selection for hemi-marsh (mean ± SE = 0.55 ± 0.04) and dense marsh (0.56 ± 0.03) over open marsh (0.14 ± 0.05; Fig. 1a). In our separate

Table 1. Model selection results for generalized linear mixed models (binomial family) with random effects for bird ID, nest ID, and a unique identifier for paired points. Results explain all, pre-flight (15–30 d post-hatch), and post-flight (31+ d post-hatch) habitat selection by fledgling Least Bitterns at Emiquon Preserve, Illinois, USA, in 2021. Lowest AICc was 579.55 for the All Ages model set, 384.05 for the Pre-Flight model set, and 174.86 for the Flight model set. K corresponds to the number of parameters per model, ΔAICc is the Akaike's information criterion corrected for small sample sizes, and w_i is the weight of the model, all models equaling 1.00 per age group.

Model	K	All ages		Pre-flight (15–30 d post-hatch)		Flight (31+ d post-hatch)	
		ΔAICc	w_i	ΔAICc	w_i	ΔAICc	w_i
Habitat Openness + Mean Emergent Veg. Height	7	0.00	1.00	0.00	1.00	0.00	0.93
Habitat Openness	6	19.34	0.00	35.51	0.00	5.98	0.05
Water Depth + Mean Emergent Veg. Height	6	25.94	0.00	22.71	0.00	7.58	0.02
Mean Emergent Veg. Height	5	30.58	0.00	33.43	0.00	10.09	0.00
Intercept Only (Random Selection)	4	69.04	0.00	73.27	0.00	24.74	0.00
Water Depth	5	70.88	0.00	74.43	0.00	19.79	0.00

analysis of dominant vegetation type, we also found all fledglings were selecting for persistent emergent vegetation (β ± SE = 0.72 ± 0.21; i.e., *Typha* spp., *Scirpus* spp.) and selecting against floating leaved (−0.35 ± 0.17; i.e., *Nelumbo lutea*) and other (−3.69 ± 1.44; i.e., non-persistent emergent or woody vegetation and mudflat) vegetation (Table 3).

We collected data at 162 Least Bittern fledgling locations and 162 paired points during the pre-flight period, and 69 fledgling locations and 69 paired points during the post-flight period. The additive effects of habitat openness and emergent vegetation height were strongly supported for both periods ($w_i = 1.00$ and $w_i = 0.93$; Table 1). Pre-flight fledglings had a higher probability of being associated with taller emergent vegetation in all cases and with dense marsh (mean ± SE = 0.58 ± 0.04) over hemi-marsh (0.47 ± 0.05) while they were found to avoid open marsh habitat (0.03 ± 0.03)

(Fig. 1b). Post-flight fledglings were associated with taller emergent vegetation and hemi-marsh (mean ± SE = 0.69 ± 0.07) over dense marsh habitat (0.50 ± 0.07) but used open marsh habitat more than pre-flight fledglings (0.24 ± 0.08; Fig. 1c). In our separate analyses of dominant vegetation type, pre-flight fledglings were positively associated with persistent emergent vegetation (β ± SE = 1.37 ± 0.31) and negatively associated with floating leaved vegetation (−1.06 ± 0.28); however, post-flight fledglings did not appear to select any vegetation type and only selected against other vegetation (−4.02 ± 1.45) (Table 3).

Fledgling survival

We radio-tagged 50 Least Bittern fledglings to monitor survival from 15 to 40 d post-hatch in 2020 and 2021; however, 6 fledglings were omitted from analyses because of tag loss during the first interval

Table 2. Coefficient estimates (β) and 95% confidence intervals for variables in best ranked generalized linear mixed models (binomial family) explaining all, pre-flight (15–30 d post-hatch), and post-flight (31+ d post-hatch) habitat selection by fledgling Least Bitterns at Emiquon Preserve, Illinois, USA, in 2021.

Predictor variable	All ages		Pre-flight (15–30 d post-hatch)		Flight (31+ d post-hatch)	
	β	95% CI	β	95% CI	β	95% CI
Mean emergent veg. height (cm)	101.00	68.00 to 133.00	161.00	106.00 to 216.00	130.00	64.00 to 199.00
Open marsh[a]	−2.36	−3.14 to −1.58	−3.80	−5.82 to −1.79	−1.64	−2.62 to −0.66
Hemi-marsh[b]	−0.14	−0.55 to 0.28	−0.45	−0.93 to 0.03	0.64	−0.18 to 1.47
Dense marsh[c]	0.33	0.07 to 0.58	0.37	0.08 to 0.66	0.18	−0.35 to 0.71

[a] Open marsh habitat is defined as open water or aquatic bed interspersed with 0–30% cover by emergent vegetation.

[b] Hemi-marsh habitat is defined as open water or aquatic bed interspersed with 40–60% cover by emergent vegetation.

[c] Dense marsh habitat is defined as open water or aquatic bed interspersed with 70–100% cover by emergent vegetation. Dense marsh habitat was reported as the intercept model, or reference category all models were compared against.
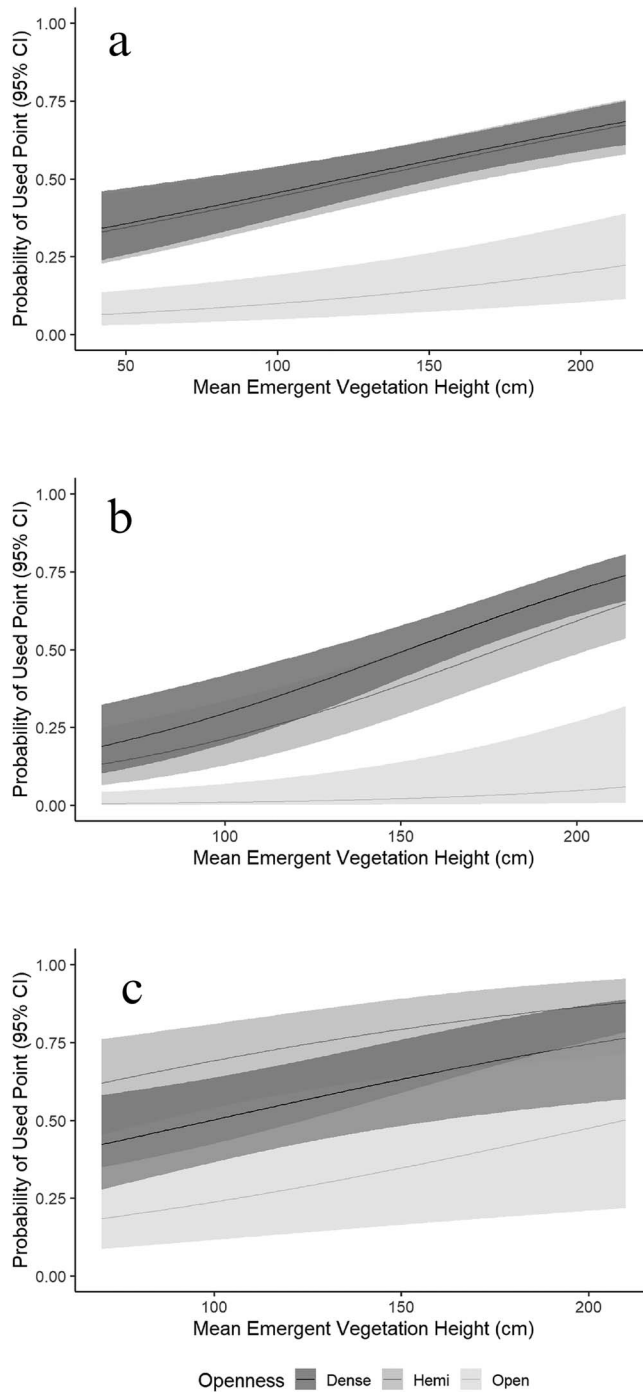
Figure 1. Probability of habitat use for (a) all post-fledging Least Bitterns (*n* = 34), (b) pre-flight (15–30 d post hatch) post-fledging Least Bitterns (*n* = 34), and (c) post-flight (31+ d post-hatch) post-fledging Least Bitterns (*n* = 26) in 2021 at Emiquon Preserve, Illinois, USA, as a function of mean emergent vegetation height (cm) and habitat openness (open marsh, hemi-marsh, dense marsh).

Table 3. Coefficient estimates (β) and 95% confidence intervals from bias-reduced logistic regression for variables of dominant vegetation type explaining all, pre-flight (15–30 d post-hatch), and post-flight (31+ d post-hatch) dominant vegetation type selection by fledgling Least Bitterns at Emiquon Preserve, Illinois, USA, in 2021.

Variable	All ages		Pre-flight (15–30 d post-hatch)		Flight (31+ d post-hatch)	
	β	95% CI	β	95% CI	β	95% CI
Persistent Emergent Vegetation[a]	0.72	0.31 to 1.13	1.37	0.79 to 1.99	0.50	−0.28 to 1.31
Floating Leaved Vegetation[b]	−0.35	−0.69 to −0.02	−1.06	−1.63 to −0.54	0.21	−0.24 to 0.66
Other Vegetation[c]	−3.69	−8.54 to −1.69	−1.51	−6.39 to 0.72	−4.02	−8.87 to −1.97

[a] Persistent emergent vegetation is defined as *Typha* spp. and *Scirpus* spp.
[b] Floating leaved vegetation is defined as *Nelumbo* spp. or other. Floating leaved vegetation was reported as the intercept model, or reference category all models were compared against.
[c] Other vegetation is defined as non-persistent emergent, woody, or submerged (i.e., mudflat).

with no signs of depredation (tags remained within a few meters of where fledglings were captured and released). Of the remaining 44 fledglings, 4 (9.1%) died between 0 and 11 d post-fledging (mean ± SE = 3.5 ± 5.1 d) and 40 (90.9%) survived until the radio-tag fell off or the bird left the site. One mortality had evidence of predation (i.e., limbs and feathers were found near the located radio-tag) and 3 mortalities were likely due to exposure (i.e., the carcass had no evidence of predation and the radio-tag was still attached). Predator identity could not be determined from the located remains. Potential predators include raccoons, American minks, and fox snakes (Schmidt et al. 2023). Post-fledging survival was best explained by a model that included the additive effects of age (β = 0.34; 95% CI = 0.01–0.69) and year (β = 3.04; 95% CI = −0.77 to 5.31; w_i = 0.77; Table 4). Daily survival was lowest in

2020 and immediately following fledging (Fig. 2). Daily survival rates of fledglings in 2020 and 2021 correspond to 2 week survival estimates of 88.1% and 98.6%, respectively. We did not find any habitat variables that were strong predictors of survival (Table 4).

Discussion

Following fledging, Least Bitterns selected dense habitats with tall emergent vegetation, not unlike the habitat Least Bittern adults select for nesting (Lor and Malecki 2006). Studies of post-fledging habitat use in grasslands and forest have also found selection for dense vegetated habitat, presumably to decrease predation risk while also providing refuge from adverse weather conditions (Small et al. 2015, Jones et al. 2017). Least Bittern fledglings also used persistent emergent

Table 4. Model selection results for the logistic exposure regressions of Least Bittern post-fledging survival at Emiquon Preserve, Illinois, USA, in 2020 and 2021. The lowest reported AIC was 39.13.

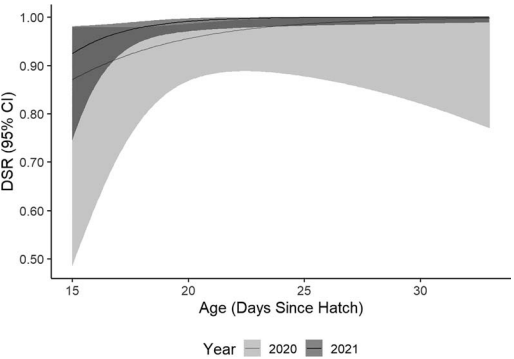| Model	K	ΔAICc	w_i
Year + Age	3	0.00	0.77
Year	2	3.37	0.14
Age	2	4.77	0.07
Constant Survival	1	9.48	0.01
Water Depth	2	10.83	0.00
Habitat Openness	3	10.90	0.00
Distance from the Nest	2	11.34	0.00
Day of the Year	2	11.37	0.00
Water Depth + Habitat Openness	4	11.99	0.00
Dominant Vegetation	3	12.24	0.00

Figure 2. Daily survival rate (DSR) of post-fledging Least Bitterns (n = 44) in 2020 and 2021 at Emiquon Preserve, Illinois, USA, as a function of age (days since hatch) and year.

vegetation over emergent floating leaved vegetation and non-persistent and woody vegetation types, and anecdotal observations indicate that while in dense herbaceous vegetation they were found beneath the cover of lotus or cattail leaves and rarely exposed. These findings support the idea that fledglings select habitat with greater cover and fewer canopy gaps for greater predator protection (Small et al. 2015, Raybuck et al. 2020).

As expected, fledgling habitat use appears to be dependent on age and mobility. We found that pre-flight fledglings (15–30 d post-hatch) selected denser habitat than those that could fly (31+ d post-hatch). Pre-flight fledglings are likely less adept at evading predators and benefit from remaining in taller and denser vegetation while they complete development, and dense vegetation to hold onto with their feet may also assist in their mobility until they attain flight (Anders et al. 1997, Jones and Bock 2005, Jones et al. 2017). As they gained flight, fledglings transitioned into more open spaces (i.e., hemi-marsh, open marsh), suggesting that the ability to fly may allow them to exploit areas with abundant food but less cover (Moore et al. 2009, Darrah and Krementz 2010, Fisher and Davis 2011, Small et al. 2015, Jones et al. 2017).

Post-fledging survival is highly variable across species of birds (23–87% 3 weeks post-fledging), and in some species fledgling survival has a greater impact on population growth than other demographic parameters (Anders et al. 1997; Todd et al. 2003; Fisher and Davis 2011; Cox et al. 2014, 2019). The low mortality observed in our study contrasts with other studies of open-nesting birds; however, high fledgling survival has also been seen in wetland birds such as American Black Ducks (*Anas rubripes*; 97.4%; Long-core et al. 1991), Harlequin Ducks (*Histrionicus histrionicus*; 99.0%; Regehr 2003), and Wood Storks (*Mycteria americana*; 96.5%; Hylton 2004) in the first 2 weeks post-fledging. Most mortality in our study was due to exposure rather than predation, again contrasting from studies of open-nesting forest and grassland passerines where predation was the leading cause of fledgling mortalities (Sullivan 1989, Naef-Daenzer et al. 2001, Yackel Adams

et al. 2006, Jones et al. 2017). The low post-fledging mortality and few predation-caused deaths of Least Bitterns could be a direct result of a combination of factors including water deep enough to deter terrestrial predators such as raccoons (Schmidt et al. 2023) and selection of dense habitats (Bogner and Baldassarre 2002, Hoover 2005, Jones and Bock 2005).

As with other post-fledging studies, mortality risk was greatest in the 3 d following fledging (Yackel Adams et al. 2006, Raybuck et al. 2020). Studies have frequently demonstrated a post-fledging bottleneck in altricial and semi-altricial birds, with elevated mortality in the first week following fledging that abruptly decreases and reaches an asymptote at low mortality/high survival (Jones et al. 2016, Naef-Daenzer and Grüebler 2016, Jones et al. 2020). The greatest threats immediately following fledging are predation, starvation, and exposure due to a lack of experience foraging, avoiding predators, and selecting habitats with access to food (Ricklefs 1969, Newton 1998, Naef-Daenzer et al. 2001, Hylton 2004). These threats are probably greatest in the short period when younger birds lack the ability to fly away when threatened and instead remain still in an attempt to avoid detection or when habitat conditions are poor around the nest and they are unable to efficiently disperse to areas with greater protection from the elements or access to food resources, but survival rate increases as flight is attained and their ability to disperse increases (Sullivan 1989, Anders et al. 1997, Cox and Kesler 2012, Bates and Ballard 2014). Our observations support the hypotheses above, and we recorded Least Bitterns that were unable to fly adopting the bill-up stance typical of bitterns aiding in camouflage, whereas Least Bitterns that could fly typically flew away once detected by our team. Further, Least Bitterns who likely died of exposure were collected from mudflats and anecdotal records suggest there was little to no water found within their age-dependent range of daily dispersal.

All mortalities but one were observed in 2020, which may be a result of habitat changes caused by a large intensity dewatering at Emiquon Preserve between June and August 2020 that removed 1.4 m

of water. Floodplain wetlands' historical dependence on overbank flooding to reset wetland succession has been replaced by water management regimes to mimic these historical flood pulses (Dahl 1990, Havera et al. 1997). Fluctuating water levels may be a natural hurdle for Least Bittern fledglings. In an ever-increasing agricultural and urban landscape where wetland loss is ubiquitous, intensive dewatering that removes water below nests may reduce survival of Least Bitterns immediately following fledging (Dahl 1990, Platteeuw et al. 2010, Wallace et al. 2011). Dewatering management during the breeding season has also been found to remove standing water beneath many marsh bird nests, leading to greater predation risk, particularly by mammals (Schmidt et al. 2023). For young fledglings with low mobility, the removal of water below and around the nest they are leaving could place these birds at risk of death due to exposure, starvation, or predation. Keeping this in mind, our study revealed only one loss due to predation and overall post-fledging survival was ultimately high. However, our results are derived from a relatively small sample size suggesting further studies should be conducted to determine appropriate habitat conditions and management actions impacting predation risk and other causes of mortality.

Although we did not find habitat factors that influenced survival, the presence and extent of water at larger scales can be important for creating viable nesting habitat, preventing terrestrial predator access to the marsh interior, and controlling the abundance and availability of prey for young waterbirds, so more work is needed on the complex relationships between water-level management and fledgling survival (Picman et al. 1993, Gawlik 2002, Jedlikowski et al. 2015). Prey availability can also impact survival, mass, and growth of fledglings (Neaf-Daenzer et al. 2001, Neaf-Daenzer and Gruebler 2016, Cox et al. 2019) and is an important avenue for future research in Least Bittern. In this study we focused on the first 2 weeks of the post-fledging period, as many birds left our study site between 2 weeks and 1 month post-fledging. Given that our study looked at a small frame of time within the post-fledging period, more research is needed to understand where fledglings are moving after 1 month, what habitat decisions they are making, and how these decisions impact their mortality. A juvenile bird's first migration and winter can also be hazardous as the bird is not experienced in handling additional stressors including exhaustion, lack of useable habitat, and extreme weather conditions (Kersten and Brenninkmeijer 1995, Wiens et al. 2006, Borkhataria et al. 2012, Geary et al. 2015), so more work is needed to assess survival and habitat use as young birds reach independence and engage in their first fall migration and winter.

While research and management decisions often focus on the nesting period, the post-fledging period can be as or more important given that individuals spend as much or more time in this stage (Anders et al. 1998, Burke et al. 2017, Jones et al. 2017). In a previous study focused solely on nest survival, we found management, such as active dewatering, outside of critical Least Bittern nesting stages can create suitable nesting habitat while limiting predation risk at nests (Schmidt et al. 2023). In the present study, we also suggest wetland management that creates densely vegetated inundated habitats during the post-fledging period may support an increased survival of fledgling Least Bitterns and continue to provide habitat for adult Least Bitterns.

Conflict of interest statement

Author contributions

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