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Photo: Eliacim Agosto-Torres

Survival and movement patterns of the Endangered *Agelaius xanthomus* (Yellow-shouldered Blackbird) during the post-fledging period

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Cover Page: A pair of recently fledged *Agelaius xanthomus* (Yellow-shouldered Blackbird) siblings approximately 6 m from their nest. Picture taken in the Pitahaya mangrove forest, Cabo Rojo, Puerto Rico on 9 August 2023 by Eliacim Agosto-Torres.

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Abstract

This study provides insight into the post-fledging period of *Agelaius xanthomus* (Yellow-shouldered Blackbirds), including measurements of morphology, survival rates, behavioral patterns, and movement ecology. The results provide valuable information on the early life stages of this Endangered species and contribute to a better understanding of its conservation and management. Specifically, we present the results of a two-year study that sought to determine the survival and movement patterns of 51 individuals of *A. xanthomus* during the post-fledging period in southwestern Puerto Rico during the 2019 and 2020 breeding seasons. Fledglings had black plumage with yellow shoulder patches, similar to adults, but with less gloss. Morphometric analysis showed that there was no difference in mass or tarsus length between the two years. However, older siblings within nests were significantly larger than their younger counterparts at the time of fledging. Survival analysis revealed six recorded deaths, most of which occurred within the first two days of fledging. Deceased fledglings were always the underdeveloped youngest siblings of the nest and were unable to sustain flight over long distances. Behavioral observations revealed fledgling roosting patterns and a gradual reduction in parental care. The study revealed an intriguing phenomenon in which non-parental helpers assisted fledglings by providing food but withdrew their support as the fledglings matured. In addition, tagged fledglings exhibited seemingly coordinated movements toward communal roosts at multiple sites. As the first post-fledging study of *A. xanthomus*, and one of the few studies of its kind conducted in the Caribbean, this work provides a critical baseline on survival, movement, and care during this vulnerable stage, directly addressing key management concerns and offering region-wide insight into the challenges *A. xanthomus* fledglings face in human-altered coastal landscapes.

Keywords

Agelaius xanthomus, home-range, movement patterns, post-fledging survival, Yellow-shouldered Blackbird

Resumen

Patrones de supervivencia y movimiento del amenazado *Agelaius xanthomus* (Mariquita de Puerto Rico) durante el período de volantón • Este estudio proporciona información del período de volantón de *Agelaius xanthomus* (Mariquita de Puerto Rico), e incluye mediciones morfológicas, tasas de supervivencia, patrones conductuales y ecología de sus movimientos. Los resultados brindan información muy importante sobre las primeras etapas de vida de esta especie amenazada y contribuyen a una mejor comprensión de su conservación y manejo. Presentamos, específicamente, los resultados de un estudio de dos años cuyo objetivo fue determinar los patrones de supervivencia y movimiento de 51 individuos de *Agelaius xanthomus* durante el período de volantón en el suroeste de Puerto Rico en las temporadas reproductivas del 2019 y 2020. Los volantones tenían un plumaje negro con parches amarillos en los hombros, similar a los adultos, pero menos brillantes. El análisis morfométrico mostró que no existieron diferencias en la masa corporal o la longitud del tarso entre años. Sin embargo, los pichones mayores dentro del mismo nido fueron significativamente más grandes que sus hermanos más jóvenes en el momento de abandonar el nido. El análisis de supervivencia registró seis muertes, la mayoría de las cuales ocurrieron dentro de los dos primeros días posteriores

al abandono del nido. Los volantones muertos siempre fueron los hermanos más jóvenes y menos desarrollados de la nidada y que fueron incapaces de mantener vuelos de largas distancias. Las observaciones conductuales revelaron patrones en el uso de dormideros por parte de volantones, así como una reducción gradual del cuidado parental. El estudio reveló un fenómeno intrigante en el cual los individuos ayudantes no parentales asistían a los volantones proporcionándoles alimento; el cual iban retirando gradualmente conforme estos alcanzaban mayor madurez. Asimismo, los volantones marcados exhibieron movimientos aparentemente coordinados hacia dormideros comunales en múltiples localidades. Como el primer estudio centrado en la etapa de volantón de *A. xanthomus*, y uno de los pocos de este tipo llevados a cabo en el Caribe, este trabajo brinda una línea base crítica sobre la supervivencia, los movimientos y el cuidado durante este estado vulnerable. Además, aborda directamente las principales preocupaciones para el manejo y ofrece una perspectiva regional en los retos que enfrentan los volantones de *A. xanthomus* en paisajes costeros alterados por el hombre.

Palabras clave

Agelaius xanthomus, Mariquita de Puerto Rico, patrones de movimiento, rango de hábitat, supervivencia del volantón

Résumé

Survie et déplacements d'*Agelaius xanthomus* (Carouge de Porto Rico), une espèce en danger, au cours de la période suivant l'envol •

Cette étude donne un aperçu de la période qui suit l'envol pour *Agelaius xanthomus* (Carouge de Porto Rico), notamment par des mesures de la morphologie, des taux de survie, des modèles comportementaux et de l'écologie des déplacements. Les résultats fournissent des informations précieuses sur les premiers stades de vie de cette espèce menacée et contribuent à une meilleure compréhension de sa conservation et de sa gestion. Ainsi, nous présentons les résultats d'une étude de deux ans qui visait à déterminer les taux de survie et les schémas de déplacement de 51 individus d'*Agelaius xanthomus* après l'envol, dans le sud-ouest de Porto Rico au cours des saisons de reproduction 2019 et 2020. Les jeunes à l'envol ont un plumage noir avec des taches jaunes sur les épaules, semblable à celui des adultes, mais moins brillant. L'analyse morphométrique a montré qu'il n'y avait pas de différence de masse ou de longueur de tarse entre les deux années. Cependant, les frères et sœurs les plus âgés des nichées étaient significativement plus grands que leurs cadets au moment de l'envol. L'analyse de la survie a révélé six décès enregistrés, dont la plupart se sont produits dans les deux premiers jours suivant l'envol. Les oisillons décédés étaient toujours les plus jeunes et les moins développés de la nichée et n'étaient pas capables de voler sur de longues distances. Les observations comportementales ont révélé le regroupement des jeunes en dortoirs et une réduction progressive des soins parentaux. L'étude a mis en évidence un phénomène intrigant dans lequel des aidants non parentaux accompagnaient les oisillons en leur fournissant de la nourriture, puis réduisaient leur soutien à mesure que les jeunes grandissaient. En outre, les jeunes marqués ont montré des déplacements apparemment coordonnés vers des dortoirs communs sur plusieurs sites. En tant que première étude sur *A. xanthomus* après l'envol et l'une des rares études de ce type menées dans la Caraïbe, ce travail fournit une base de référence essentielle sur la survie, les déplacements et les soins au cours de cette phase de vulnérabilité, abordant directement les principales préoccupations en matière de gestion et offrant un aperçu à l'échelle régionale des difficultés auxquels sont confrontés les jeunes *A. xanthomus* dans les paysages côtiers modifiés par la présence humaine.

Mots clés

Agelaius xanthomus, Carouge de Porto Rico, domaine vital, schémas de déplacement, survie après l'envol

Breeding success is a fundamental component in the study of avian population dynamics (Nur and Sydeman, 2009). Not only does it determine the trajectory of bird populations, but it also serves as a powerful indicator of the health and viability of avian ecosystems (Clutton-Brock 1988, Newton *et al.* 2008). Thus, understanding the complexities of breeding success is critical for avian conservation. Historically, the primary metrics used for these estimates have been nest and fledging success. While undeniably important, these metrics may, however, not capture the full range of challenges faced by young birds (Ricklefs 1969, DeSante and George 1994). Therefore, relying on these traditional measures could inadvertently lead to an incomplete or oversimplified understanding of avian reproductive dynamics, especially if other critical life stages, such as the post-fledging stage, are overlooked (Streby and Andersen 2011).

The post-fledging period, which begins after nest departure and culminates in the attainment of parental independence, is full of challenges (Kershner *et al.* 2004). The inexperience of young birds, coupled with their limited mobility, makes them particularly vulnerable to a range of threats, which includes predation and environmental stressors (Anders *et al.* 1997, Kershner *et al.* 2004). However, the inherent challenges of locating

and monitoring fledglings have resulted in this life-stage being one of the least studied in avian ecology (Farnsworth *et al.* 2001). This oversight can be significant: if conservation and management strategies are designed without consideration of the post-fledging stage, such strategies may not fully address factors critical to juvenile survival and eventual recruitment into adult populations (Donovan and Thompson 2001, Streby and Andersen 2011).

Deepening our understanding of survival and spatial ecology during the post-fledging period is paramount to holistic bird conservation. Knowing the intricate details, such as physiological traits that ensure survival, habitat characteristics preferred by fledglings, and broader environmental factors, can inform conservation strategies with a precision that is currently lacking (Taylor and Norris 2010). Identifying and mitigating the risks associated with the post-fledging stage, combined with insights into the spatial behavior of fledglings, can foster a nuanced understanding of habitat use, migration patterns, and resource availability (Donovan and Thompson 2001, Farnsworth *et al.* 2001). Such understanding is even more important in light of recent trends observed in *Agelaius xanthomus* (Yellow-shouldered Blackbird) populations.

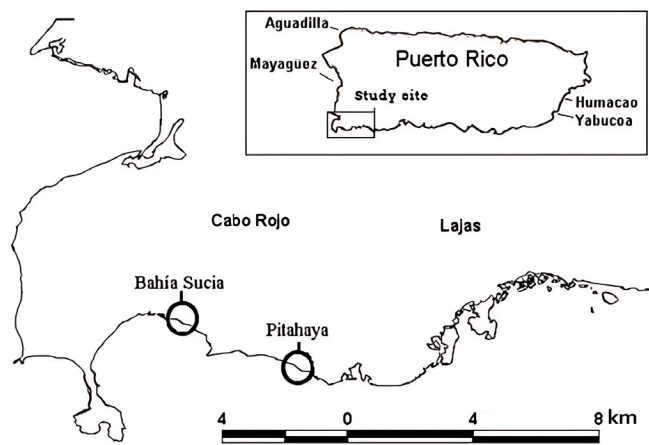


Fig. 1. Location of the study area within Puerto Rico, highlighting Bahía Sucia and the Pitahaya Mangrove Forest locations. Image modified from López-Ortiz (2019).

A. xanthomus, commonly known as "Mariquita de Puerto Rico" or "Capitán", is a songbird endemic to the archipelago of Puerto Rico (Raffaele *et al.* 1998). It is characterized by having a shiny dark plumage that is contrasted by deep, rich, golden-yellow humeral patches (Post 2020). This species was once considered abundant in the San Juan area and common throughout the lowlands of the main island of Puerto Rico, Vieques, and Mona Island (Taylor 1864, Wetmore 1927, Post 1981, Raffaele 1989, Wiley *et al.* 1991, Raffaele *et al.* 1998, Post 2020). However, habitat loss due to agricultural and urban development, and a significant decline in reproductive success due to brood parasitism by the invasive *Molothrus bonariensis* (Shiny Cowbird) (Post 1981, Cruz *et al.* 1985, Post and Wiley 1976, Post and Wiley 1977, Cruz *et al.* 2005, Post 2020) have restricted this species to four main areas scattered throughout the archipelago: Mona Island, the municipality of Ceiba, the municipality of Salinas, and the southwestern region of Puerto Rico (i.e., the municipalities of Cabo Rojo and Lajas). This has resulted in the species being classified as Endangered since 1976 (BirdLife International 2020) with the current world population currently estimated at approximately 1,200 individuals (JPGC unpubl. data).

Since the 1980s, conservation efforts of *A. xanthomus* have successfully addressed the challenges of brood parasitism by *Molothrus bonariensis* (Wiley *et al.* 1991). While these efforts have resulted in a population increase, the stabilization or plateauing of this growth (López-Ortiz 2019) requires a reassessment of the current challenges. If brood parasitism is no longer the predominant limiting factor, it is conceivable that high mortality during the post-fledging period may be the emerging constraint (Taylor and Norris 2010, Streby *et al.* 2016). Studying this, in line with the recovery goals set for *A. xanthomus*, is therefore of paramount importance (Anders *et al.* 1997, Donovan and Thompson 2001). The specific objectives of this work were to: (1) Estimate post-fledging mortality rates, (2) quantify fledgling home-range sizes, and (3) assess whether variation in mortality and home-range size is driven by interannual differences or individual morphological traits.

Methods

Study site

This study was conducted in the southwestern region of Puerto Rico, in the municipalities of Cabo Rojo and Lajas. These areas are considered subtropical dry forest life zones according to Holdridge's life zone system (Miller and Lugo 2009). This study was conducted in the areas locally known as the Pitahaya Mangrove Forest (17°57'06.6"N, 67°06'27.4"W) and the areas surrounding Bahía Sucia (17°57' 50.5"N, 67°10'05.6"W) (Fig. 1). Both areas have been consistently used for nesting by *Agelaius xanthomus* throughout the breeding season. Particularly, the Pitahaya Mangrove Forest is the primary nesting habitat for the species on the main island of Puerto Rico (Post 2020) and is also designated as critical habitat (USFWS 1976, 2011). This site stretches approximately 6.5 km along the coast, and is the largest mangrove stand in the southwestern region of Puerto Rico. It is characterized by the presence of *Rhizophora mangle* (red mangrove) fringe forest and a basin forest of *Rhizophora mangle*, *Avicennia germinans* (black mangrove), and *Laguncularia racemosa* (white mangrove) (Garcia *et al.* 1998). On the other hand, Bahía Sucia is composed of a 7.5 km long mangrove fringe along the coast surrounding a salt flats area. Annual precipitation for both sites ranges between 41 and 127 cm, with the majority of the rainfall occurring between the months of April and November (Western Regional Climate Center 2025). There are currently over 250 Artificial Nesting Structures (ANS) in the Pitahaya Mangrove Forest and around 25 in Bahía Sucia (USFWS 2011). In the case of the structures in the Pitahaya Mangrove Forest, they are distributed throughout the site and placed about 5 m from the *Avicennia germinans* fringe to avoid predation by rats. Notably, about 60% of these ANS are positioned in front of dead *A. germinans* fringes, providing virtually no canopy cover. However, the structures in Bahía Sucia are located in the easternmost part of the site and are placed about 5 m from a live *Rhizophora mangle* fringe.

Nestling handling and tagging procedures

Agelaius xanthomus typically nests in the study area between the months of May and September, therefore, ANS monitoring began in the first week of May of each breeding season (2019 and 2020) and continued on a weekly basis until all studied individuals had been tagged, which occurred on 26 July 2019 and on 2 August 2020. Nestlings were captured opportunistically during ANS surveys conducted by Puerto Rico Department of Natural and Environmental Resources staff at the Pitahaya Mangrove Forest and Bahía Sucia. These surveys were usually conducted in the morning by walking along the edges of *Avicennia germinans* (Pitahaya Mangrove Forest) and *Rhizophora mangle* (Bahía Sucia) mangroves while monitoring ANS.

Only nestlings that were at least 14 days old, had a minimum weight of 16 g, and did not attempt to fledge while being captured were tagged in this study. All nestlings were above the mass threshold, though there were three that fledged as we approached the nest, and although we did tag their siblings, these individuals were excluded from the study. This resulted in 51 nestlings within 37 nests in our sample (24 nests had 1 chick, 10 nests had 2 chicks, 2 nests had 3 chicks, and 1 nest had 4 chicks). Morphometric data were collected when nestlings were estimated to be within 72 hours of fledging, with a median

of 1 day before fledging (range = 0–3). We measured mass, wing chord, and tarsus length. Nestling siblings were sometimes at different developmental stages (Fig. 2). For the less developed individuals with feathers in sheaths, we still measured wing chord but acknowledge that these values do not represent final wing chord since feathers were still growing. Nestlings were banded on the right leg with a metal band bearing a unique identification number. Nestlings were not sexed, as this was not possible visually. We tagged nestlings with a 0.75 g Very High Frequency transmitter using the breast harness method described by Thaxter *et al.* (2014). For the 2019 season, we used Holohil® BD-2 transmitters, while the 2020 nestlings were tagged with A1035 ATS® transmitters. After processing, the nestlings were returned to their nests (Fig. 3).

For age analyses, we used a binary within-nest classification to represent competition pressure: nestlings with no older sibling at the time of capture was classified as “older,” and nestlings with ≥ 1 older sibling was categorized as “younger.” In nests

with three or four chicks, only the single oldest nestling was classified as “older,” and all others were classified as “younger.” By definition, all individuals from single-chick nests were also classified as “older.” We recognize that including single-chick nests and pooling all non-oldest siblings as “younger” may limit direct within-nest contrasts and dilute age-specific differences; accordingly, statistical estimates of the age effect should be interpreted as conservative, within-nest contrasts of competition pressure rather than effects of nest size or exact age. Biologically, the resulting age effect should be interpreted as the effect of having at least one older and potentially bigger competitor for food, not as an effect of exact age among multiple younger chicks or of nest size per se.

We performed two-way ANOVA in the R programming language (R Core Team 2021) to assess for effects of study year (2019 vs 2020), age, and their interaction on mass, wing chord, and tarsus length, using $\alpha = 0.05$ as the threshold for statistical significance. This approach allowed for an assessment of the main effects of age and year, as well as their interaction, on the nestlings' physical attributes.

Monitoring and radiotelemetry

We monitored radio-tagged birds using a three-element Yagi antenna and a handheld 148–174 MHz receiver. In addition to this, because most adults at our study sites had been previously banded with metal USGS bands, we could reliably identify the parents of some monitored nestlings and fledglings by photographing the band number. Fledglings were tracked immediately after they had successfully fledged, approximately 14–19 days after hatching. A few nestlings fledged immediately after being returned to their nest after transmitter placement ($n = 5$ individuals), while the majority fledged within the next 1–3 days ($n = 46$). Not all nestlings within a nest fledged at the same time. Each fledged bird was located using the homing-in technique (Kenward 2000) three to four days a week, with most fledglings being located once in the morning and once in the afternoon, whenever possible with multiple locations sometimes recorded on each visit, for the duration of the transmitter's battery life or until the fledgling perished. Each fledgling was located on 18–24 separate days in 2019 and 39–52 separate days in 2020 (Table 1), while each fledgling was tracked over a period of 30–34 days in 2019 and 55–69 days in 2020. The entire period during which we tracked individuals was 28 May to 15 September in 2019 and 3 June to 11 October in 2020. Upon relocation, we observed each individual for approximately 20 min and recorded aspects of their behavior, including begging, being fed, perching location, ability to fly, and attendance by adults. We stopped tracking an individual if we deemed them to have completed the post-fledging period (i.e., they were not observed receiving parental care such as feeding or protection over three consecutive encounters). If transmitter signals originated from hard-to-access areas, like dense *Rhizophora mangle* fringes, the fledgling's location was estimated, and the bird was revisited on a subsequent day. Following the protocol established by White Jr. *et al.* (2005), if telemetry data indicated that a fledgling remained stationary in such areas for at least three consecutive tracking days, a concerted effort was undertaken to visually verify its status. While most tracking activities were conducted during daylight



Fig. 2. *Agelaius xanthomus* nestling siblings, showing different stages of feather development. Photograph taken in the Pitahaya Mangrove Forest by Jean P. González-Crespo on 2 July 2020.



Fig. 3. *Agelaius xanthomus* nestling inside an artificial nesting structure (ANS) at Bahía Sucia. This nestling seemed to be ready to fledge in the next 72 hours. Photograph taken in Bahía Sucia by Eliacim Agosto-Torres on 13 June 2019.

Table 1. Home range size estimates and morphometric measurements of radio-tracked fledgling *Agelaius xanthomus* in southwestern Puerto Rico during the 2019 and 2020 breeding seasons ($n = 22$ individuals). All morphometric data were collected before fledging. MCP = minimum convex polygon; KDE = kernel density home range estimation. Morphometric data were collected as nestlings 0–3 days before fledging. "D" denotes individuals with still developing wing feathers at time of measurement.

Fledgling ID	Breeding Season	Weight (g)	Tarsus (mm)	Wing chord (mm)	95% MCP (ha)	50% KDE (ha)	Age at fledging (days)	Nest ID	Number of individual days tracked
V1	2019	26.81	24.99	58 ^D	162.70	227.90	17	18	23
V6	2019	34.85	25.61	78	16.10	31.70	19	186	22
V7	2019	28.90	24.45	72	10.60	34.80	18	182	23
V8	2019	28.85	22.75	68	9.60	27.60	17	125	23
V9	2019	29.35	24.14	75	23.40	60.70	18	14	24
V10	2019	24.93	24.61	60 ^D	12.10	41.60	15	14	20
V11	2019	25.31	24.31	62 ^D	49.20	189.90	19	208	21
V13	2019	27.80	24.70	63	63.80	244.00	18	215	22
V16	2019	24.76	24.17	63	24.10	90.30	15	240	20
V18	2019	24.57	24.45	59 ^D	70.40	418.80	16	112	18
V20	2019	23.00	21.87	62 ^D	188.00	650.30	17	36	23
V24	2019	20.43	24.10	71	29.20	110.80	16	54	22
V27	2019	25.06	25.74	61 ^D	147.80	404.50	16	70	23
V29	2019	27.13	24.42	63	84.10	409.30	19	120	20
V30	2020	27.41	24.10	58 ^D	11.30	41.30	16	34	43
V33	2020	21.15	21.40	58 ^D	142.40	868.30	17	59	46
V35	2020	22.53	24.40	69	44.30	170.60	15	187	39
V36	2020	32.18	24.10	78	65.10	170.00	18	187	39
V39	2020	25.14	23.50	58 ^D	68.50	280.40	17	64	52
V41	2020	31.43	25.40	64	137.80	635.30	19	131	48
V44	2020	18.07	22.60	55 ^D	8.30	165.90	15	215	51
V45	2020	23.42	21.30	52 ^D	1569.60	1274.20	16	45	49

hours, some individuals were also tracked at night, specifically between 1900 and 0200, to assess if parental care extended into these hours.

Home range and movements

We used the *adehabitatHR* (Calenge 2024) and *sp* (Pebesma and Bivand 2005, Bivand *et al.* 2013) packages within R to generate two estimates of home range sizes (i.e., the area traversed by an individual animal in its normal activities)—95% Minimum Convex Polygon (MCP) and 50% Kernel Density Estimation (KDE) (Cruz-Burgos 1999, Puente-Rolón 1999). Home range estimates (both 95% MCP and 50% KDE) included all location fixes recorded for each fledgling from the first night they reached and

used their nocturnal roost onward, excluding earlier movements toward that roost which reflected parental following rather than established home range behavior. In instances where there was more than 75% overlap between siblings' locations, only one home range estimation, selected at random, was used. Furthermore, fledglings with an insufficient number of relocations (i.e., less than 30 relocations), due to either transmitter loss, battery depletion, or death, were excluded from home range estimation. We created dynamic movement maps using *tidyverse* (Wickham *et al.* 2023), *moveVis* (Bartkowski and Schwalb-Willmann 2022), and *magick* (Ooms 2023) to visualize fledgling movement patterns over time at the two sites (Supplemental Data 1). The animations are composed of multiple frames, with each

frame representing the fledgling's location at a single tracking encounter. Tracking encounters occurred at approximately two-day intervals; therefore, each successive frame corresponds to movement over a two-day period rather than a single calendar day.

We ran linear regression models to evaluate the relationships between home range size and weight and tarsus length. Wing chord was not included in this analysis due to a large number of nestlings still having developing wing feathers. We also performed a two-way ANOVA to assess how home range size was influenced by study year, age, and their interaction.

Survival analysis

Using the Kaplan-Meier estimator, as detailed in Pollock *et al.* (1989) and White Jr. *et al.* (2005), we computed daily survival probabilities of tagged fledglings during the post-fledging period. This analysis was executed using the survival package (Therneau 2024). For each individual, the analysis window began on the date of fledging and concluded either when we determined that the fledgling was no longer receiving parental care or the presumed date of death. When birds neared the end date of their transmitter's battery life and could not be located despite multiple days of searching, they were censored under the assumption that the transmitter had ceased functioning but the bird remained alive. We also used the survival package to estimate cumulative survival across the post-fledging period for each season. To compare survival rates between the two breeding seasons, we used the "survdiff()" function within the survival package to conduct a log-rank test.

Results

Morphometrics

During the two-year period, 51 individuals were tagged at the study sites, with 29 fledglings tagged in 2019 ($n = 22$ nests) and 22 in 2020 ($n = 15$ nests). All fledglings had black plumage with yellow patches on the shoulders, resembling adults but less glossy. The mean mass (\pm S.E.) of nestlings was 26.14 ± 0.76 g in 2019, and 24.88 ± 1.09 g in 2020. Mean wing chord measurements (\pm S.E.) were 63.41 ± 1.28 mm in 2019, and 59.36 ± 1.47 mm in 2020 (but note these include feathers that were still growing). The mean tarsus lengths (\pm S.E.) were 24.43 ± 0.26 mm in 2019, 23.81 ± 0.34 mm in 2020. A two-way ANOVA revealed no significant effect of year on mass ($F = 0.12$, $df = 1$, 47 , $p = 0.733$), wing chord length ($F = 2.31$, $df = 1$, 47 , $p = 0.135$), or tarsus length ($F = 1.62$, $df = 1$, 47 , $p = 0.209$). However, there was a significant effect of age on mass ($F = 4.97$, $df = 1$, 47 , $p = 0.031$), indicating that older nestlings are generally heavier than younger ones. On the other hand, there were no significant effects of age on wing chord length ($F = 2.41$, $df = 1$, 47 , $p = 0.127$) or tarsus length ($F = 1.71$, $df = 1$, 47 , $p = 0.197$), and no significant interaction between age and year for wing chord length ($F = 0.28$, $df = 1$, 47 , $p = 0.599$), tarsus length ($F = 0.01$, $df = 1$, 47 , $p = 0.924$), and mass ($F = 0.79$, $df = 1$, 47 , $p = 0.378$), indicating that the observed age differences were consistent across both years of the study.

Our direct observations of 38 fledging events revealed flight capability differences between older and younger siblings. Twenty-seven of these events were of older siblings, and of these, 81% successfully flew to the edge of the mangrove forest

upon fledging. For the eleven individuals that were younger siblings, only 18% managed the same. This difference was significant ($X^2 = 10.714$, $df = 1$, $p = 0.001$). Regardless of age, the fledglings unable to reach the mangrove forest edge often fell into the water. However, of the 14 that fell into the water, 100% were able to swim the approximately 3–8 m to the mangrove forest edge in less than 2 min. We observed some individuals floating on the water's surface, seeming to take breaks before continuing to swim until they reached the forest edge.

Home range and movements

Of the 51 individuals tagged (from 36 nests), we estimated home range sizes for 22 individuals (from 20 nests). The others were excluded because of $> 75\%$ home range overlap with a sibling ($n = 6$ individuals excluded, $n = 5$ nests affected) or due to us not being able to record at least 30 locations ($n = 23$ individuals excluded, $n = 20$ nests affected). Home range sizes were highly variable between individuals (Table 1). For the 14 fledglings tracked in 2019, MCP mean home range size (\pm S.E.) was 63.6 ± 16 ha (range = 9.6–188 ha), while for the 8 tracked in 2020, MCP mean home range was 256 ± 189 ha (range = 8.3–1569.6 ha). Although the transmitters deployed in 2020 lasted close to two months compared to those from 2019, which lasted only one month, there was no apparent transmitter effect on fledgling home range size. This is because home range size stabilized in 22 ± 2.3 days in 2019 and 21 ± 1.4 days in 2022, after which, home range size did not change drastically with time. A two-way ANOVA revealed that there was no significant effect of age ($F = 2.56$, $df = 1$, 18 , $p = 0.127$), year ($F = 3.53$, $df = 1$, 18 , $p = 0.077$), or their interaction ($F = 3.60$, $df = 1$, 18 , $p = 0.074$) on MCP home range size. When home range was estimated using KDE, similar patterns were observed. The mean home range (\pm S.E.) was 228 ± 55.1 ha (range = 27.6–650.3 ha) for those tagged in 2019 and 391 ± 163 ha (range = 41.3–1274.2 ha) for those tagged in 2020. A two-way ANOVA again showed no significant effect of age ($F = 0.22$, $df = 1$, 18 , $p = 0.645$), year ($F = 3.68$, $df = 1$, 18 , $p = 0.071$), or their interaction ($F = 0.81$, $df = 1$, 18 , $p = 0.380$) on KDE home range size.

The large range in home range size among the 2020 fledglings was driven by one individual (V45) with an MCP of 1,569.6 ha and a KDE of 1,274.2 ha. To determine whether the non-significant differences between years were influenced by this outlier, we re-ran the analyses excluding V45. For MCP, mean home range (\pm S.E.) now was 68.2 ± 20.6 (range = 8.3–142.4 ha) and a two-way ANOVA excluding V45 again showed no significant effect of age ($F = 1.39$, $df = 1$, 17 , $p = 0.255$), year ($F = 0.01$, $df = 1$, 17 , $p = 0.939$), or their interaction ($F = 0.17$, $df = 1$, 17 , $p = 0.688$). For KDE, mean home range (\pm S.E.) now was 333 ± 114 (range = 41–868 ha) and the two-way ANOVA excluding V45 likewise showed no significant effect of age ($F = 0.19$, $df = 1$, 17 , $p = 0.666$), year ($F = 1.25$, $df = 1$, 17 , $p = 0.278$), or their interaction ($F = 0.13$, $df = 1$, 17 , $p = 0.726$).

Nestling mass, and tarsus length were not significantly correlated with MCP home range size ($R^2 = 0.2607$, $F(3, 18) = 2.12$, $p = 0.134$). Individually, none of the predictors had a significant effect on home range size (mass, $\beta = 10.6$, $SE = 19.6$, $t = 0.54$, $p = 0.596$; tarsus length, $\beta = -132.7$, $SE = 66.6$, $t = -1.99$, $p = 0.062$). In contrast, when examining KDE home range size,

these same morphological variables collectively explained 33.95% of the variation ($R^2 = 0.3395$, $F(3, 18) = 3.08$, $p = 0.054$). Here, neither tarsus length ($\beta = -123.8$, $SE = 61.2$, $t = -2.02$, $p = 0.058$) or mass ($\beta = 0.80$, $SE = 18.0$, $t = 0.04$, $p = 0.967$) had a significant effect on home range size.

Fledglings from different locations exhibited distinct, unidirectional movement patterns that led to the discovery of communal nocturnal roosts. Fledglings at the Pitahaya Mangrove Forest ($n = 38$) had an eastward trajectory, whereas those from Bahía Sucia ($n = 13$) exhibited a westward movement (Supplemental Data 1). These coordinated movements culminated at previously unidentified communal roosts, which were also frequented by other bird species, such as *Quiscalus niger* (Greater Antillean Grackle). These roosts were *Rhizophora mangle* mangrove islands about 10–15 m from the shore or mangrove fringe. During their navigation to these roosts, fledgling *Agelaius xanthomus* moved through the outer edges of *Rhizophora mangle* and *Avicennia germinans* mangrove habitats. Once reaching the communal roosts, fledglings would follow their presumed parents to foraging areas and would return to the same communal roost at night. On average, the distance between fledglings' foraging areas, which were located in places distinct from the original nesting sites, and these nocturnal roosts (\pm S.E.) was $6,207 \pm 796$ m, ranging from 1,193 to 13,821 m ($n = 22$). This behavior persisted until the end of the transmitters' battery life or fledglings achieved parental independence. Nevertheless, the use of these communal roosts ceased at the end of the breeding season.

Survival analysis

Six of the 51 radio-tagged fledglings died during the study period (three each in 2019 and 2020). This resulted in an estimated cumulative survival rate (\pm S.E.) of 0.897 ± 0.06 for the first 34 days post-fledging in 2019 and 0.870 ± 0.07 for the first 69 days in 2020. There was no difference in cumulative survival rate between years (Chi-square = 0.1, $df = 1$, $p = 0.80$). A closer look at the survival curves (Fig. 4) shows that five of the six mortality events occurred within the first two days post-fledging and the remaining event occurred on the third day. Each of the six deceased fledglings (i.e., V17, V28, V29, V31, V43, and V48) were the youngest sibling of a two-nestling clutch, were less developed compared to their older sibling (Table 2, 3), and fell into the water when fledging. All dead fledglings were recovered in areas of dead mangrove with minimal cover and no visible signs of predation (Fig. 5).

Behavioral observations

During the first eight days after leaving the nest, fledglings sat still on low branches (less than 3 m above the ground) in trees or bushes, *Avicennia germinans* mangrove pneumatophores, or other types of vegetation growing close to the ground. They rarely flew and were constantly begging for food whenever either parent was around. Between day 9–18 post-fledging, fledglings could sustain longer flight distances at a time (more than 45 m). They spent most of their time perched on branches in the canopy foraging independently, but would still beg for food whenever they approached one of their parents. By about 20 days after leaving the nest, the plumage of all the fledglings resembled that of an adult. At this point, the fledglings could fly

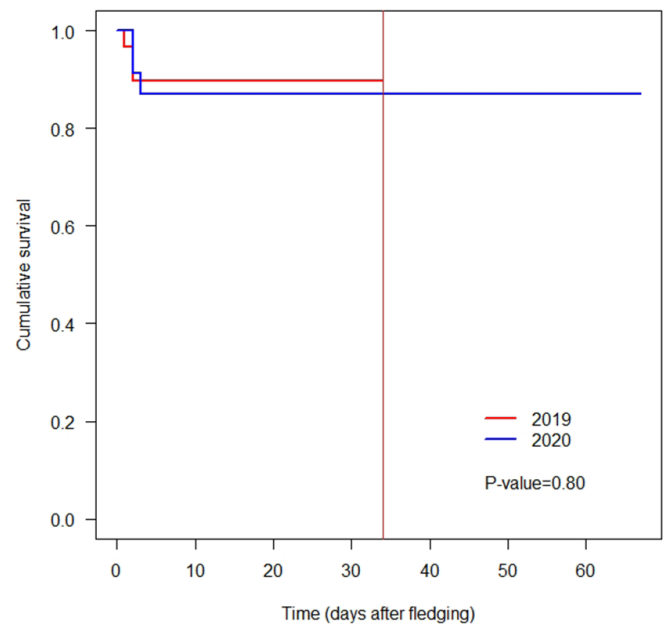


Fig. 4. Kaplan-Meier survival curves (solid lines) for radio-tagged *Agelaius xanthomus* (Yellow-shouldered Blackbird) fledglings in 2019 (red line; $n = 29$ birds) and 2020 (blue line; $n = 22$ birds). The brown vertical line shows the 34-day mark where 2019 fledglings were censored. The y-axis shows the cumulative proportion of fledglings that survived during the monitoring period, and the x-axis shows time to event, or the amount of time an individual was monitored before it died, lost its signal, or its transmitter was recovered. See Methods section for details.

with the same capacity as an adult and could only be identified as young birds by their begging call and behavior. For approximately the first 21 days, parents would respond immediately to a fledgling's begging for food, while feeding intensity then declined gradually, dropping markedly around days 30 to 40. Fledglings at this age would still beg from their parents but were often ignored for relatively long periods of time (> 15 min). Nevertheless, we observed parents still feeding their young up to 62 days post-fledging.

At dusk, young birds who were still unable to fly long distances were observed roosting on or near the same tree they had been at sunset. These young birds would ascend to the canopy and nestle into the foliage until daylight. This behavior was consistent even among siblings; when present together they would choose the same roosting site. Parental care was completely absent during the night. Adults left at sunset to gather at a separate communal roost, returning to their fledglings at dawn. If the fledglings were able to reach the communal roost, they would join their parents and leave at dawn with them.

During our observations of *Agelaius xanthomus*, we saw several instances of non-parental individuals ("helpers") feeding fledglings. These helpers were present at four of the 37 monitored broods (11%), and we documented a maximum of three helpers assisting a single fledgling, whereas the remaining aided broods each had one or two helpers. Specifically, these helpers

were observed providing food alongside the parents, feeding five of the tagged fledglings, two of which were siblings while the other three were unrelated. We were able to confirm the presence of helpers through the observation of other banded adults assisting in the feeding process or by witnessing three or more adults feeding a single chick simultaneously. In one instance, we observed two parents and three helpers feeding a fledgling, with the adults confirmed to be different birds by their leg band IDs. In the remaining cases, we confirmed two parents and either one or two helpers providing food. We did not track whether these helpers assisted multiple nests, nor did we know their identities, such as whether they could be offspring from previous years, as we were only able to confirm that they were simply not the fledglings' parents. However, this assistance was not perpetual. Helping ceased approximately 30 days post-fledging. Fledgling provisioning then returned entirely to the parents, emphasizing the temporary nature of the helpers' role.

Discussion

Morphometrics

Comparative morphometric measurements from southwestern Puerto Rico showed no significant inter-annual differences in wing chord, tarsus length, or body mass. This morphological stability suggests that nestling traits in these areas were unaffected by short-term environmental fluctuations or year-to-year variation during the study period, which was to be expected since both seasons did not differ markedly in local rainfall or food resources (JPGC unpubl. data). The observed uniformity across annual variables may reflect stable developmental conditions during the nestling period. While all traits are influenced by both genetic and environmental factors (Ricklefs 1969), such consistency could benefit individuals by enhancing fledgling survival during the vulnerable post-fledging stage. For example, adequate body mass provides energy reserves needed for early independence (Griesser 2013), and well-developed tarsi and wings aid in locomotion and foraging efficiency (Martin 1987). This pattern is consistent with other avian work showing that inter-annual differences in nestling morphometrics typically emerge when years differ strongly in weather or food supply (Pérez *et al.* 2016), whereas cohorts developing under similar conditions

show comparable sizes across years (Sauve *et al.* 2021).

Despite the absence of interannual differences in morphometric traits, we observed significant mass differences between older and younger siblings within the same brood. Given that *Agelaius xanthomus* hatch asynchronously (Post 2020), some variation in nestling size is expected due to age-related differences in development. However, several observations suggest that food availability and in-nest competition also contribute to size disparities in this species. For example, three tagged siblings (V23, V24, and V26) fledged at similar ages (16–18 days), yet exhibited substantial differences in mass, ranging from 16.4 to 32.6 grams. These disparities likely reflect unequal access to food during the nestling period. Conversely, nestling V47, which had no siblings, weighed less than 17 grams when fledging at 17 days old, suggesting that spatial variation in habitat quality, temporal fluctuations in food availability, and potential differences in parental experience when foraging may also influence the development of chicks. These patterns are consistent with the brood reduction hypothesis, which proposes that asynchronous hatching can serve as a reproductive strategy under variable resource conditions, allowing parents to maximize reproductive success when resources are abundant, while minimizing investment in later-hatched chicks under scarcity (Lack 1947, Stoleson and Beissinger 1995). Similar patterns of in-nest competition and size disparity have been documented in other avian species, including *Erithacus rubecula* (European Robin), *Vireo atricapilla* (Black-capped Vireo), and *Phoenicopiterus roseus* (Greater Flamingo) (Newton *et al.* 1989, Clutton-Brock 1991, Mock and Parker 1997). In this study, the observed mass differences were mirrored by functional traits: heavier, older siblings exhibited more advanced plumage and observable superior flying ability at the time of fledging, potentially enabling them to reach protective mangrove edges more easily than their lighter siblings, thus a suite of advantages that could translate into higher post-fledging survival (Newton *et al.* 2008, de la Hera *et al.* 2009).

Suspected high levels of sibling competition in *A. xanthomus* nests may help explain why brood parasitism by *Molothrus bonariensis* has had such a severe impact on the species' decline as the added burden of raising a cowbird chick likely intensifies already intense competition among nestlings. Post (2020) observe that *M. bonariensis* eggs typically hatch within a range of 10 to 15 days, possibly outpacing *A. xanthomus* eggs which can take more than 13 days to hatch (Post and Wiley 1977, Post 2020). This advantage may allow the *M. bonariensis* chick(s) to dominate the food that's being delivered to the nest, potentially starving the younger, and potentially smaller, *A. xanthomus* nest-mates and reducing overall fledging success (Briskie and Sealy 1990, McMaster and Sealy 1998). Therefore, the continued control of brood parasitism in *A. xanthomus* nests is essential to prevent additional losses of nest productivity. In addition, complementary measures, such as food supplementation, could improve fledging success for these nests. By increasing the amount of food that chicks receive, nestling mortality could potentially be reduced and post-fledging survival improved (Donald 2007). In the case where food supplementation proves insufficient, a head-start program that temporarily rears these under-weight nestlings to a more favorable weight could also boost recruitment.



Fig. 5. Tagged *Agelaius xanthomus* fledglings found dead. (A) This fledgling was still alive during the morning of day 2, so we assume that it died on day 2 or 3. We recorded its death as of day 3, so this picture was taken two days after it had died, five days after fledging. Photograph taken at the Pitahaya Mangrove Forest on 17 June 2019. (B) This fledgling was found dead after not being able to successfully fly to nearby mangroves after fledging. Photograph taken at the Pitahaya Mangrove Forest on 16 August 2020. Both photographs by Jean P. González-Crespo.

Table 2. Summary data for *Agelaius xanthomus* fledglings captured in Southwestern Puerto Rico during the 2019 breeding season ($n = 29$ individuals). All morphometric data were collected before fledging. "D" denotes individuals with still developing wing feathers at time of measurement. "U" denotes individuals who had an untagged sibling at the time of fledging.

Fledgling ID	Weight (g)	Tarsus (mm)	Wing chord (mm)	Nest ID	Age of Fledging (days)	Hatch Order
V19	19.44	22.87	58 ^D	11	14	1/1
V2	22.52	26.54	56 ^D	12	18	1/1
V9	29.35	24.14	75	14	18	1/2
V10	24.93	24.61	60 ^D	14	15	2/2
V1	26.81	24.99	58 ^D	18	17	1/1
V20	23.00	21.87	62 ^D	36	17	1/1
V22	27.41	24.96	62 ^D	41	16	1/1
V23	32.65	25.42	68	54	18	1/3
V24	20.43	24.10	71	54	16	2/3
V26	16.43	22.69	51 ^D	54	16	3/3
V27	25.06	25.74	61 ^D	70	16	1/1
V21	33.53	25.80	66	72	18	1/1
V12	27.40	26.50	64	81	15	1/1
V25	21.83	23.40	68	89	17	1/1
V15	29.30	25.37	65	112	16	1/2
V18	24.57	24.45	59 ^D	112	16	2/2
V29	27.13	24.42	63	120	19	1/2
V28	24.64	25.93	61 ^D	120	18	2/2
V8	28.85	22.75	68	125	17	1/1
V5	28.88	24.33	74	132	19	1/2 ^U
V4	22.35	22.50	64	135	17	1/1
V7	28.90	24.45	72	182	18	1/1
V6	34.85	25.61	78	186	19	1/1
V11	25.31	24.31	62 ^D	208	19	1/1
V3	27.12	26.60	66	212	16	1/1
V13	27.80	24.70	63	215	18	1/2
V17	24.28	23.68	57 ^D	215	17	2/2
V14	28.50	25.41	64	240	16	1/2
V16	24.76	24.17	63	240	15	2/2

Table 3. Summary data for *Agelaius xanthomus* fledglings captured in Southwestern Puerto Rico during the 2020 breeding season ($n = 21$ individuals). All morphometric data were collected before fledging. "D" denotes individuals with still developing wing feathers at time of measurement. "U" denotes individuals who had an untagged sibling at the time of fledging.

Fledgling ID	Weight (g)	Tarsus (mm)	Wing chord (mm)	Nest ID	Age of Fledging (days)	Hatch Order
V37	31.59	25.4	63	11	16	1/1
V51	25.43	25.5	63	11	18	1/1
V50	27.05	25.1	61 ^D	13	17	1/1
V31	16.63	21.2	45 ^D	18	18	2/2 ^U
V30	27.41	24.1	58 ^D	34	16	1/1
V42	28.83	26.2	58 ^D	57	16	1/4
V43	19.07	22.1	61 ^D	57	18	2/4
V45	23.42	21.3	52 ^D	57	16	3/4
V46	22.48	21.2	53 ^D	57	19	4/4
V33	21.15	21.4	58 ^D	59	17	1/1
V38	32.41	23.9	59 ^D	64	18	1/3
V39	25.14	23.5	58 ^D	64	17	2/3
V40	26.80	23.7	52 ^D	64	14	3/3
V49	27.81	25.3	60 ^D	89	15	1/2
V48	25.90	25.7	58 ^D	89	17	2/2
V41	31.43	25.4	64	131	19	1/1
V47	16.51	22.7	46 ^D	182	17	1/1
V32	28.16	23.6	64	183	15	1/1
V36	32.18	24.1	78	187	18	1/2
V35	22.53	24.4	69	187	15	2/2
V34	17.42	21.6	51 ^D	210	14	1/1
V44	18.07	22.6	55 ^D	215	15	1/2 ^U

Behavioral observations

The post-fledging period in *A. xanthomus* is like other avian species, since it has a pivotal developmental phase where juvenile birds refine their motor abilities, foraging methods, and undergo a transformation in plumage (Ricklefs 1969). From days 1–8 post-fledging, fledglings clearly depend on their environment and parental care to survive. They display limited mobility and consistent begging behavior. The constant use of lower branches can be due to their underdeveloped flight muscles and feathers, and as a potential tactic to stay inconspicuous to predators (Ricklefs 1969). This aligns with Tome and Denac (2012)

who emphasized that fledglings are vulnerable during these initial days, and that they depend on cryptic behavior to increase survival probabilities. Between days 9–18, the fledglings show a marked shift towards increased autonomy, characterized by longer flight spans and the initiation of self-foraging. This transitional phase from total dependency to partial independence mirrors patterns documented in other passerine species (Ricklefs 1969). Moreover, their molting into new feathers near day 20 highlights a key maturation phase, a finding that resonates with Swaddle and Witter (1997) who observed that changes in plumage often accompany behavioral shifts in fledglings. Parental investment closely tracks this trajectory. Initially, parents are highly responsive to the fledglings' begging for food, ensuring their survival during this vulnerable phase, but provisioning decreases as juveniles master their own foraging skills. As Donazar and Ceballos (1990) explained, this could serve to push fledglings towards refining their foraging skills, effectively nudging them towards self-sufficiency. Concurrently, this diminishing attention might free parents to prepare for potential subsequent breeding or divert their energies towards their own sustenance (Williams 2018, Beedy *et al.* 2023). However, due to the length of time it takes for fledglings to become independent (i.e., up to 62 days), it seems unlikely that breeding *A. xanthomus* pairs would nest again during the same breeding season after successfully caring for fledglings.

Adult *A. xanthomus* roost communally at night (Post and Post 1987, Post 2020) and therefore do not provide nocturnal care to fledglings that have yet to reach these roosts. This could be due to adult birds prioritizing communal roosting, capitalizing on the safety it offers against nocturnal predators through the "dilution effect" which reduces individual predation risk when birds assemble in significant numbers (Parejo *et al.* 2005); something that can't be achieved if parents roost only with their fledglings. Beyond mere numbers, these roosts can serve as hubs for information exchange where birds share knowledge about food sources, potential threats, and other critical environmental cues (Ward and Zahavi 1973, Goodale *et al.* 2010). Nevertheless, our observations confirm that *A. xanthomus* fledglings eventually join these roosts as well, but they expose a consequential trade-off: until they are able to do so, fledglings are routinely left unattended overnight. These fledglings, left exposed to various threats from predators, exhibit heightened vulnerability due to their limited life experiences (Magrath *et al.* 2006). However, we recorded *A. xanthomus* fledglings mitigating this risk by climbing higher into the canopy at dusk, remaining motionless throughout the night, and descending only when the presumed parents returned at dawn; a behavior that likely minimizes detection by nocturnal predators. These findings refine our understanding of post-fledging survival constraints in this Endangered species by showing how juvenile behavior compensates for a parental strategy that favors communal safety over continuous guarding.

Our work revealed that *A. xanthomus* are facultative cooperative breeders. Cooperative breeding is a social breeding system in which more than two individuals, including at least one non-parent, provide care for offspring (Cockburn 2006). About 9% of passerines breed cooperatively (Jetz and Rubenstein 2011), but it is not common in icterids (Cockburn 2006). In our system, 11% of monitored broods had at least one helper.

The presence of helpers may provide a variety of benefits. For example, helper provisioning may contribute to higher fledgling survival rates by accelerating juvenile growth and development (Van de Loock *et al.* 2017). This assistance may also indirectly reduce the workload of the breeding pair, freeing them to engage in other important activities such as territory defense or preparation for future breeding attempts (Crick 1992). We do not know if the *A. xanthomus* helpers we observed were related to the breeding pair. However, helpers in other systems are often close relatives of the breeding pair, consistent with kin-selection theory. By aiding kin, individuals increase their indirect genetic fitness (Hamilton 1964). However, some helpers may instead be failed breeders redirecting parental care. Skutch (1961) described cases where adults continued to feed begging offspring near their unsuccessful nests. Given the low nest success reported for the species (Gonzalez-Crespo and Puente-Rolon 2021), helper behavior may reflect lingering parental impulses rather than kin-directed care. Furthermore, Liu (2015) found that 37% of *A. xanthomus* broods have extrapair paternity. This raises the possibility that some helpers may actually be parents of the fledglings they assist, a pattern observed in other cooperative breeders (Brouwer and Griffith 2019). Long-term studies using color-banding and genetic sampling are needed to understand how prevalent the behavior is and to test hypotheses about how helping is maintained in this system. The use of ANS makes this especially feasible, as they provide predictable, accessible sites for monitoring individuals and collecting repeated data across years.

We found that *Agelaius xanthomus* exhibited a post-fledging dependency that lasts between 60–70 days, roughly twice the approximately 5-week period reported for *Agelaius phoeniceus* (Red-winged Blackbird; Nero 1984). Such prolonged care likely underpins the high fledgling survival we observed, but it also demands a substantial energetic investment from adult birds. Helpers in our population contributed only during the first approximately 30 days post-fledging, after which only the parents provisioned. We hypothesize that early helper support buffers parental effort during the most critical phase and facilitate extended care, ultimately enhancing survival. This idea could be tested by comparing dependency duration and fledgling survival between broods with helpers and those without. Given the low prevalence of helpers, however, factors such as food availability and predation pressure are probably the primary drivers of fledgling dependence and survival, although none of our tagged fledglings died due to predation. Nevertheless, the occasional helper assistance may provide a valuable boost when it occurs.

Survival analysis

Fledgling survival rates showed no significant interannual differences, with rates exceeding 87% in both years. The observed similarity suggests that environmental or other external factors influencing fledgling survival may have remained relatively constant over the two study years. However, the concentration of deaths in the first three days after fledging suggests that individuals are more vulnerable in the beginning of the fledging period. This pattern, common in altricial birds, may be due to a variety of factors, including the physical challenges of first flights, navigational inexperience, or potential exposure to

environmental stressors (Cox *et al.* 2014). It could also be due to inadequate development during the nestling stage. In our system, each of the deceased fledglings was the youngest, smallest, and weakest flyer in its brood. Across bird species, the youngest or last-hatched nestlings often face the highest risks, as their smaller size and lower competitiveness puts them at a disadvantage compared to their older siblings (Stoleson and Beissinger 1995). Targeted food supplementation during the pre-fledging stage could help reduce the effects of sibling competition and improve post-fledging survival of the youngest nestling in the brood.

Habitat quality also appeared to play a key role. All dead fledglings were found in patches of dead mangrove with sparse vegetation near their ANS. It is likely that these fledglings, limited by poor flight ability, were unable to reach nearby live mangrove patches that offered better refuge. This suggests that, in addition to sibling dynamics, the availability of suitable, nearby post-fledging habitat is essential for early survival (Weatherhead 1985, Magrath 1991). Together, these findings suggest a dual approach to improving post-fledging survival: improving nestling condition through food supplementation and enhancing fledgling habitat by restoring and preserving healthy mangrove cover.

Home range and movements

Although this is the first published estimate of fledgling *A. xanthomus* home range during the post-breeding period, adult home ranges in southwestern Puerto Rico were previously reported by Cruz-Burgos (1999) to be 228.9 ± 56.2 ha during the 3 months post-breeding and 236.1 ± 42.2 ha during the 3 months pre-breeding, providing a benchmark for comparison. As expected for fledglings with limited mobility and experience, our MCP estimates were generally smaller than adult values. Apparent similarity to adult-scale ranges occurred only in 2020 and was driven by a single wide-ranging fledgling (V45; MCP = 1,569.6 ha). When this outlier was excluded, mean fledgling home range estimates using MCP are well below the adult estimates provided by Cruz-Burgos (1999).

A. xanthomus exhibits a distinctive home range and territorial system. Individuals maintain separate breeding and non-breeding home ranges that overlap only minimally and their size remains stable between seasons (JPGC unpubl. data). During the breeding season, pairs defend only the immediate nesting area until their chicks fledge. Once fledglings depart the nest and reach the communal roost, they typically follow their presumed parents to their foraging areas within the parents' breeding home range until they reach independence. Not surprisingly, when comparing their home range to other species during their post-fledgling period, *A. xanthomus* had larger home ranges when contrasted with small forest songbirds, such as *Empidonax virens* (Acadian Flycatcher) and *Cardinalis cardinalis* (Northern Cardinal) which were observed to occupy very small home ranges during the post-fledging period with a mean of 2.33 ha (95% MCP) and 0.93 ha (95% MCP) respectively (Ausprey and Rodewald 2013). However, there are fundamental differences in social organization between *Agelaius xanthomus* and these species. Unlike solitary forest songbirds, *A. xanthomus* are highly social icterids that form communal roosts and exhibit

group-based spatial dynamics, which likely contribute to their broader space use. However, when compared to larger birds, such as *Corvus kubaryi* (Mariana Crow) which had a mean home range of ~76 ha (100% MCP) (Faegre *et al.* 2019), their home ranges are of similar size. In general, interspecific differences in post-fledging home range size are expected and likely reflect species' body size, habitat structure, food distribution, and the duration of the post-fledging dependence period (Tarwater and Brawn 2010, Ausprey and Rodewald 2013, Jenkins *et al.* 2017). Nevertheless, improving our understanding of how these factors shape space use would directly inform management, especially for endangered or at-risk species, by identifying the habitats and spatial scales most critical to juvenile survival and recruitment (Cox *et al.* 2014).

Within *A. xanthomus*, morphometric predictors explained only modest, non-significant variation in home-range size: for MCP, mass and tarsus together only explained 26.1% of the variation, while they only explained 34.0% of the variation on KDE. Overall, these results suggest that morphology alone cannot predict fledgling home range size. Therefore, other factors, such as habitat structure, food distribution, and individual behavior, are likely more important at determining a fledgling's home range (Mitchell *et al.* 2010). While disentangling their effects will require fine-scale movement data paired with detailed habitat mapping, further research in this area could allow for a better understanding of the spatial ecology of *A. xanthomus* which could lead to better and more efficient conservation strategies that can improve survival and recruitment in this Endangered species (Cox *et al.* 2014). However, from our direct observations, *A. xanthomus* fledglings' home range size seemed to be influenced more by their parents' home range, as they were moving or being led by their presumed parents towards the roost or foraging areas, rather than by their morphological traits.

Fledglings extensively use *Rhizophora mangle* and *Avicennia germinans* mangroves, underscoring the importance of these habitats as vital corridors to communal roosts and foraging areas. The dense root systems and foliage of mangroves likely offer protection from ground and aerial predators (Chavez-Ramirez and Wehtje 2012), while their cooler microclimate compared to adjacent grasslands and scrublands (Krauss *et al.* 2008) may help reduce dehydration and overheating during fledgling movements. In addition, social cues, such as observing conspecifics or other species, may guide fledglings along safer routes (Goodale *et al.* 2010). Although mangroves are not the primary foraging habitat for this species (coastal forests and scrublands are their main foraging habitat throughout the year), they may still provide valuable opportunistic food sources such as insects, mollusks, and crustaceans, which are known prey items for this species (Robertson and Duke 1990, Post 2020). Given these benefits, conserving mangrove corridors that connect nesting sites to post-fledgling communal roosts and foraging areas is important for supporting post-fledgling survival and the overall recovery of the species.

Conclusion

The post-fledging period is a critical phase in the life cycle of many avian species (Cox *et al.* 2014), with survival rates during this time playing a key role in shaping population dynamics.

High fledgling mortality can significantly limit population growth, leading to declines across generations (Streby *et al.* 2011). Encouragingly, our study found that *A. xanthomus* in southwest Puerto Rico exhibited high survival rates during this vulnerable period – an optimistic sign for this Endangered species. Our observations suggest that finding suitable shelter immediately post-fledging could be the biggest challenge that fledglings face. Therefore, assuming that there are no other significant factors limiting population growth in this species, ensuring that fledglings can obtain cover during their first days after fledging should be of highest priority. This could include active restoration through mangrove planting, as well as long-term strategies to protect these habitats from development and climate-related threats.

Given that our findings suggest the post-fledging stage may not be a limiting factor for *A. xanthomus* population growth, future research should shift focus to other potential constraints on species recovery. Areas for investigation could include food availability, predation rates, and the impact of habitat loss or degradation across different life stages. Research into the population's genetic diversity and the role of helpers in reproductive success could provide insights into population viability. In parallel, implementing targeted management strategies, such as food supplementation or a head-start program to improve nestling survival warrant consideration, as these measures could potentially lead to an increase in population size. Together, these efforts could help identify and address the most pressing barriers to population growth, ultimately supporting the recovery of this Endangered species.

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Author Contributions

Conceptualization: JPGC, RLO, ARPR, KRR; data curation: JPGC, EAT; formal analysis: JPGC, EAT; investigation: JPGC, EAT; methodology: JPGC, RLO, ARPR, KRR; validation: JPGC, EAT; visualization: JPGC, EAT; writing—original draft: JPGC;

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Supplemental Data 1. Dynamic maps showing the movements of *Agelaius xanthomus* (Yellow-shouldered Blackbird) fledglings towards communal nocturnal roosts in southwest Puerto Rico during the 2019–2020 breeding seasons. (A) Eastward movements from the Pitahaya Mangrove Forest (38 individuals tracked, 12 shown); (B) westward movements from Bahía Sucia (13 individuals tracked, 1 shown).