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Eastern Whip-poor-will (*Antrostomus vociferus*) nesting ecology: behavior of nesting adults and chick growth

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ABSTRACT

Eastern Whip-poor-will (*Antrostomus vociferus*) populations have declined precipitously since 1970, yet key aspects of their breeding biology remain understudied compared to other aerial insectivores. We used trail cameras to monitor 14 whip-poor-will nests during May–August 2023 in Rhode Island, USA. We estimated sex-specific incubation constancy (number of minutes per day on the nest) and observed behavioral interactions of adults with the nest, between paired males and females, between adults and chicks, and between adults and predators during the incubation and chick rearing stages. Additionally, we quantified chick growth trajectories ($n = 12$) for nine morphometric measurements, and growth rates for the four most informative measurements. Females spent 92 ± 2% of the 24 h period incubating, while males only assisted with incubation 4 ± 4% of the time. Paired males and females displayed a rarely documented courtship-like behavior at the nest. We also observed incubating females singing the male song, an anti-predator defensive behavior, and a slug (Gastropoda) as a predator of an egg. We provide the first published estimates of chick growth for the species and generated predictions of chick size that estimated chick age to a range of 1–2 days based on four measures (mass, tarsus length, humerus length, and wing chord). Whip-poor-will growth rates were like those of similar sized nightjars (Fiery-necked Nightjar *Caprimulgus pectoralis* and Common Pauraque *Nyctidromus albicollis*) and other aerial insectivores (flycatchers, Tyrannidae; swallows, Hirundinidae). Our growth models provide a baseline for assessing the effects of habitat quality on whip-poor-will chick growth, and a valuable tool for estimating nesting phenology and enhancing survival analyses through precise age-specific survival estimates.

Ecología de nidificación del tapacaminos *Antrostomus vociferus*: comportamiento de adultos y crecimiento de polluelos

RESUMEN

Las poblaciones del tapacaminos *Antrostomus vociferus* han disminuido precipitadamente desde 1970, pero aspectos clave de su biología reproductiva siguen sin estudiarse en comparación con otros insectívoros aéreos. Se utilizaron cámaras trampas para observar 14 nidos de *Antrostomus vociferus* durante mayo–agosto de 2023 en Rhode Island, EEUU. Estimamos la constancia de la incubación

KEYWORDS
Aerial insectivores; early successional forest; estimating chick age; Gompertz model; incubation constancy

PALABRAS CLAVE
insectívoros aereos; bosque sucesional temprano; constancia de incubación; estimar edad de polluelos; modelo de Gompertz

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(número de minutos por día en el nido) en función del sexo y observamos las interacciones conductuales de adultos con el nido, entre machos y hembras en pareja, entre adultos y polluelos, y entre adultos y depredadores, durante las etapas de incubación y cuidado de los polluelos. Además, cuantificamos las trayectorias de crecimiento de los polluelos ($n = 12$) para nueve mediciones morfométricas y tasas de crecimiento para las cuatro medidas más informativas. Las hembras pasaron el 92 ± 2% de las 24 horas incubando, mientras que los machos colaboraron en la incubación solamente el 4 ± 4% del tiempo. Las parejas mostraron en el nido un comportamiento de cortejo raramente documentado. También observamos hembras cantando el canto del macho mientras incubaban, un comportamiento defensivo antidepredador, y una babosa (Gastropoda) que depredó un huevo. Proporcionamos las primeras estimaciones publicadas sobre el crecimiento de los polluelos de Antrostomus vociferus y generamos predicciones de tamaño de polluelos que permiten estimar la edad de los polluelos en un intervalo de 1–2 días con base en cuatro medidas (masa, longitud del tarso, longitud del húmero y cuerda alar). Las tasas de crecimiento de *Antrostomus vociferus* fueron similares a las de tapacaminos de tamaño similar (*Caprimulgus pectoralis* y *Nyctidromus albicollis*) y a las de otros insectívoros aéreos (Tyrannidae; Hirundinidae). Nuestros modelos de crecimiento proporcionan una línea de base para evaluar los efectos de la calidad del hábitat sobre el crecimiento de los polluelos de *Antrostomus vociferus*, y una valiosa herramienta para estimar la fenología de la nidificación y mejorar los análisis de supervivencia mediante estimaciones precisas de la supervivencia por edades.

Aerial insectivore populations are in decline across North America, likely driven by loss of breeding habitat and declines in the abundance and quality of insect prey available during the breeding season (Spiller and Dettmers 2019). These declines have led to calls for broad-scale conservation and legislative efforts designed to improve habitat and enhance protections of insects, especially during the breeding season (Nebel et al. 2020) when parents must feed their growing young. Nightjars (Caprimulgidae), a group of nocturnal aerial insectivores, include species with some of the largest population declines among the aerial insectivore guild (Rosenberg et al. 2016; Spiller and Dettmers 2019), yet their breeding biology is understudied compared to many diurnal species (e.g., swallows, swifts, and flycatchers) in part due to their nocturnal activity and their highly cryptic nature. The breeding biology of nightjars is unique among aerial insectivores in that females lay one or two eggs directly on the ground, hatchlings are semi-precocial, and provisioning takes place exclusively at night (Winkler et al. 2020). These unique aspects of their breeding biology enhance the value of investigating nesting behavior and the growth of chicks in this under-researched group of aerial insectivores.

The post-hatching period is a critical and vulnerable part of the avian life cycle during which variation in growth may influence survival to fledging and adult fitness (Langham 1972; Jonsomjit et al. 2007; Monaghan et al. 2008). Population models often require accurate estimates of nest success and nest survival (Mayfield 1961; Dinsmore et al. 2002; Johnson 2007), of which nest age is an important aspect. Nest age can be determined by aging nestlings or chicks as long as the age-specific growth trajectories of certain morphometric measurements (e.g., mass or tarsus length) are known (e.g., Ammann 1982; Wails et al. 2014; Sanchez et al. 2021). Nestling or chick age estimated from morphometric measurements can then be used to determine nesting phenology (Nilsson et al. 2011) and enables more accurate estimates of age-specific nest and nestling or chick survival (Wails et al. 2014). Understanding nesting phenology is especially important as climate change effects become stronger because changes in nesting phenology may result in phenological mismatch that may contribute to or worsen population declines (Jones and Cresswell 2010; English et al. 2018; Youngflesh et al. 2023).

The Eastern Whip-poor-will (*Antrostomus vociferus*, hereafter whip-poor-will) is a species of nightjar that breeds throughout the eastern United States and southeastern Canada. Whip-poor-will populations have declined by approximately 70% since 1970 (Rosenberg et al. 2016), which is thought to be primarily caused by the loss of early successional habitat (Tozer et al. 2014) and reductions in flying insect prey throughout their breeding range (English et al. 2017). Like other nightjars, whip-poor-wills are under-studied. Much of the research on whip-poor-wills has focused on occupancy and movement ecology of adults (e.g., Tozer et al. 2014; Farrell et al. 2017, 2019; Grahame et al. 2021; Spiller and King 2021; Korpach et al. 2022; Bakermans and Vitz 2024). Some studies have focused on whip-poor-will nesting ecology (e.g., Mills 1986; Akresh and King 2016; English et al. 2018; Souza-Cole 2021; Stewart 2023), but only two report the behavior of undisturbed breeding pairs around the nest (Arnold 1937; Raynor 1941), and there are currently no studies that have quantified chick growth. Arnold (1937) and Raynor (1941) reported repeated measurements of single chicks near Michigan Biological Station in Pellston, Michigan, and in Long Island, New York, respectively. Fowle and Fowle (1954) reported repeated measurements of two chicks in Algonquin Park, Ontario. The first objective of our study was to describe behavioral interactions of adults with the nest, between paired males and females, between adults and chicks, and between adults and predators during the incubation and chick rearing stages and provide estimates of sex-specific incubation constancy. The second objective was to quantify chick growth trajectories from morphometric measurements and then generate predictions of chick size (by age) for a subset of these morphometric measurements, to facilitate estimation of chick age. We also compared the chick growth rates of whip-poor-wills to those of other aerial insectivores.

Methods

Study sites

From May to August 2023, we searched for nesting Eastern Whip-poor-wills across five study sites within local and state conservation areas in Rhode Island, USA: Arcadia Management Area (41.57806°N, 71.72230°W), Francis Carter Preserve (41.43517°N, 71.67792°W), Great Swamp Management Area (41.45303°N, 71.59103°W), Marion Eppley Wildlife Refuge (41.52900°N, 71.57696°W), and Tillinghast Pond Management Area (41.64828°N, 71.76285°W) (Fig. 1). These sites were being actively managed to create or maintain early successional forest habitat for wildlife and singing whip-poor-wills were present. All five sites included stands with mature second-growth forest, early successional forest, as well as areas with open grassland. The size of each site varied depending on the size

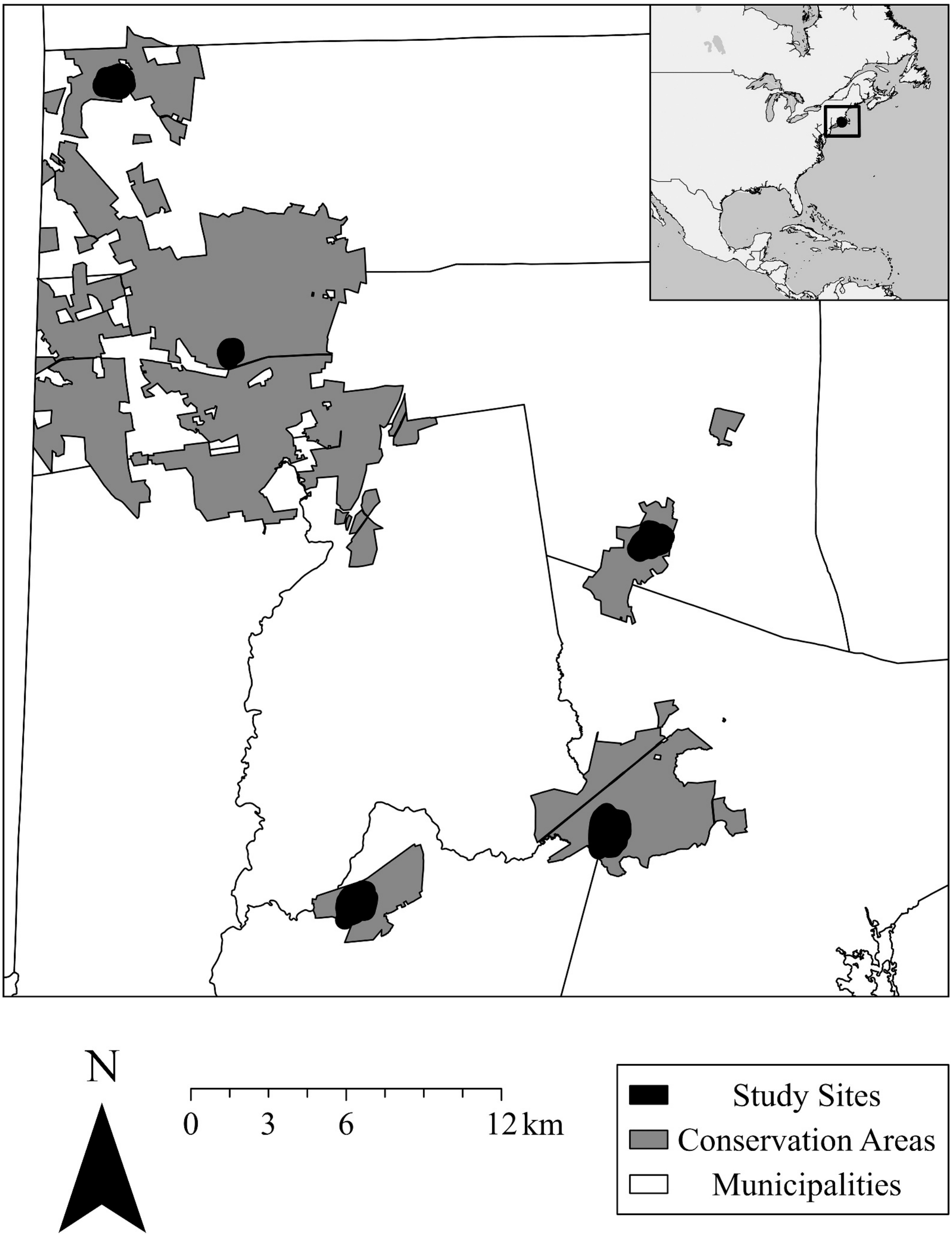

Figure 1. Study site locations in Rhode Island, USA. Study sites in order from north to south: Tillinghast Pond Management Area, Arcadia Management Area, Marion Eppley Wildlife Refuge, Great Swamp Management Area, Francis Carter Preserve. The inset map shows Rhode Island (black point inside black square) within eastern North America.

of the grassland and early successional forest openings present; the smallest site was ~51 ha and the largest was ~152 ha.

Nest finding and monitoring

To locate nests, we conducted weekly daytime walking surveys throughout the breeding season (May–Aug) that involved thoroughly searching all accessible areas at each of our five study sites. We successfully located 14 nests (including three renests) during the incubation stage across all sites and monitored 12 of those nests with trail cameras. Of these 12 nests, eight were monitored until the chicks moved away from the nest site (usually around 7 days old) at three of our five sites (Arcadia Management Area, Marion Eppley Wildlife Refuge, and Tillinghast Pond Management Area). Two of the nests were presumed predated (i.e., eggs gone) before we were able to place a trail camera, and the other four were preyed upon or abandoned within a few days of being detected. We used Browning Dark Ops Extreme and Strike Force Extreme trail cameras set to motion capture ultra quality 20–30 s video clips with a delay of 5 s between captures and fast trigger speed. Trail cameras were mounted on 1.3 × 61 cm rebar and placed 0.5–1.5 m away from the nests depending on vegetation cover. We visited the monitored nests every 2–3 days (weather dependent) to download trail camera video, confirm egg hatching, and measure chicks. To minimize potential impacts of our presence at the nests, we approached nests using different paths each visit and spent a maximum of 2 min at nests during incubation. We reviewed all trail camera video and documented interactions of adults with the nest, between paired males and females, adults and chicks, and adults and predators during both the incubation and chick rearing stages. We used the four nests with the most reliable and continuous trail camera video (at least eight full days) to calculate sex-specific incubation constancy (number of minutes per day on the nest), the average time (min) females spent away from the nest at dusk, dawn, and at night over a 24 h period, and how often males visited the nest each day.

Chick measurements

During early growth, we identified individuals by marking the legs of the chicks with different color marker until they were old enough to be banded (around 7 days old). We took nine morphometric measurements on 12 chicks from the eight monitored nests, four of which only produced a single chick. The nine measurements included mass, tarsus length, bill length from nares, posterior and anterior bill width, mouth width, humerus length, tail length, and wing chord. We followed the methods described in Pyle (1997) for measuring mass, tarsus length, bill length from nares, anterior bill width, tail length, and wing chord. Measurements for posterior bill width were taken just behind the nares, mouth width measurements were taken at the corners of the mouth, and humerus length was measured from the tip of the bone at each end of the humerus. We collected the complete set of measurements on all 12 chicks at almost all nest visits conducted every 2–3 days (Supplemental Table S1 reports daily mean sizes and sample sizes for each measurement). Mass was measured using a portable digital scale to the nearest 0.1 g, tail length and wing chord were measured using a standard wing chord ruler to nearest millimeter, and all other lengths were measured using vernier calipers to the nearest 0.1 mm. We spent a maximum of 10 min measuring chicks at a given nest to minimize disturbance to the adult female and chicks.

Statistical analysis

For our growth analysis of each of the nine morphometric measurements, we used the Gompertz growth model to calculate growth trajectories from hatching to fledging (0–15 days old; English et al. 2018):

$$f(t) = ae^{-be^{-ct}}$$

where $f(t)$ is the value of each variable (e.g., mass, tarsus, etc.) at time t (in days), a is the upper asymptote, b sets the displacement of the curve along the x-axis, c is the growth rate coefficient, and e is Euler's number. The Gompertz model is widely used for many avian growth analyses (e.g., Ricklefs 1967; Tjørve and Underhill 2009; Garrido-Bautista et al. 2023). We modeled the Gompertz growth equation in a Bayesian framework using the brms package (Bürkner 2017) in *R* 4.1.0 (www.rproject.org, R Core Team 2021). We used this method to enhance the robustness of our analysis given our small sample size. The models were constructed using wide, diffuse priors (a normal distribution with mean 0 and standard deviation of 100) and random effects for individuals for all parameters to account for individual variation in growth patterns. Each model was implemented using a Gaussian likelihood and estimated via a Markov Chain Monte Carlo (MCMC) algorithm with four parallel chains, each run for 10,000 iterations. The first 5,000 iterations of each chain were used as warm-up and discarded, resulting in a total of 20,000 posterior samples for inference. We checked for model convergence by visually inspecting the four parallel MCMC trace plots and considered the Gelman-Rubin diagnostic ($\hat{R}$, Gelman 2004) <1.05 to indicate convergence. Posterior predictive check plots were visually inspected to assess model fit, and leave-one-out R^2 (LOO-R^2) was used to evaluate the predictive performance of the growth models, with mean LOO-R^2 estimates ≥0.94 used to identify which of the nine growth models were most informative.

Maximum growth rates and the days at which they occurred were predicted for the most informative measurements. The first derivative of the Gompertz growth model defines the growth rate at any time t:

$$f'(t) = abce^{-be^{-ct}}e^{-ct}$$

Growth rates of each variable for each day from 1–15 were predicted using the posterior distribution of the parameter estimates from the models. By predicting the growth rates for each day individually, we were able to determine the day at which the growth rate was highest.

To predict the mass and size of chicks for each day for the purpose of estimating age of unknown-aged chicks, we used the posterior predictions from each of the final, most informative models to generate mean size and mass estimates with 95% credible intervals for each day. Given that the most precise estimates of chick age up to 15 days old may be obtained with multiple rather than single measurements, we also averaged the posterior predictions from the most informative measurements to generate an estimate of chick age based on these combined measures.

Results

Adult and chick behavior

Nest defense

When we approached nests and chicks throughout incubation and prior to chick fledging, females would often engage in a broken wing display once flushed off the nest. Females flushed easily during the early stages of incubation and became more reluctant to flush from the nest close to hatch and after chicks hatched. Sometimes females would forgo the broken wing display and fly to a close perch and vocalize soft “quirt” calls while watching us as we were at the nest or measuring chicks. Chicks started exhibiting a threat display during nest visits starting around 4–5 days old. The display involved spreading their wings out parallel to the ground and lunging forward with mouth agape. Chicks were more likely to do this threat display the older they were.

Incubation period

Throughout the day and at night, females primarily remained motionless during incubation although they regularly (three or more times per hour) shifted their position on the eggs or the eggs themselves using their feet or bill, to preen, or to stretch their wings and tail (Supplemental Video S1); these behaviors lasted up to several minutes before they settled again. Additionally, incubating females exposed to direct sunlight fluttered their gular flap for extended periods, presumably to thermoregulate. Males incubated eggs only at night and exhibited the same behaviors seen in the females. The four nests that had the most reliable and continuous trail camera video supplied recordings for a total of 40 days, covering days 4–17 of incubation, from which we estimated incubation constancy of males and females. On average, females spent 92 ± 2% (mean ± SD) of the 24 h period incubating eggs compared to 4 ± 4% in males. Incubating females left the nest habitually at dusk and dawn (leaving and returning at similar times each day), spending on average 41 ± 13 min ($n = 40$, mean ± SD) away from the nest at dusk and 27 ± 12 min ($n = 38$) away from the nest at dawn. Females less frequently left the nest at night (40% of days monitored) compared to dawn and dusk, but when they did leave at night, their incubation recesses were longer (126 ± 85 min; $n = 16$). Males often visited the nest at dusk (58% of days monitored) and occasionally at dawn (23% of days monitored) with incubation time lasting on average only 7 ± 4 min ($n = 23$) and 15 ± 10 min ($n = 9$), respectively. Males replaced females on the nest almost every time the females left at night (94% of nights) for extended periods of time, spending on average 124 ± 87 min ($n = 15$) incubating. Males and females directly interacted at the nest on 73% of the 40 days that the four nests were continuously monitored.

Several unusual behaviors of males and females were documented during incubation. We observed incubating females at four of the 12 monitored nests sing up to ten times in sequence at dusk, at dawn, and at night (Supplemental Video S2). The songs were the full “whip-poor-will” vocalization documented in males. We also observed one incubating male singing up to 15 times immediately before he departed the nest. During the incubation period, males and females often directly interacted at the nest at dusk, at dawn, and at night although occasionally (27% of the time) males arrived at the nest to take a turn incubating after the females had departed. When males and females were present at the nest together, they engaged in a pair-bonding display (Supplemental Video S3). The display generally began with the male arriving at the nest which triggered the female to repeatedly grunt ("gur-gur-gur") while raising her tail and rocking back and forth. The male typically responded to the female's display with a two-note vocalization ("ku-ong") one or more times and then reciprocated the grunting vocalization but without the movement displayed by the females. Most interactions ended with the female leaving the nest followed by the male incubating. On a few occasions, a female arrived while the male was still incubating. In these few cases, the display roles were reversed with the male grunting at the female and doing the movement display while the female responded vocally.

We observed eight instances on the trail camera video of direct interactions between incubating female whip-poor-wills and perceived predators including one common raccoon (*Procyon lotor*), one eastern chipmunk (*Tamias striatus*), one eastern milk snake (*Lampropeltis triangulum*), one unknown vertebrate, two slugs, and one snail (Gastropoda), and one American giant millipede (*Narceus americanus*). In every case, the females faced the perceived predators, extended both wings up at a steep angle, fanned out their tails, and rocked back and forth (Supplemental Video S4). Only the raccoon prompted a female to flush from the nest, which resulted in the raccoon chasing after the female and away from the eggs, with the raccoon never returning to the nest (Supplemental Video S5). The encounter with the snake was the only instance when an incubating female engaged in an additional active defense behavior beyond that described above (Supplemental Video S6). As the snake approached, the female paced around the nest in the defensive stance described above, occasionally struck the ground with her wings, and grunted. The snake struck at the defending female several times, missed her in each instance, and within a few minutes was successfully driven off. Out of these eight documented encounters, an egg was predated in only one, and it was by a slug. The trail camera video showed the female in the defensive stance while the slug was on the egg (Supplemental Video S7); the next day we visited the nest and found a small hole in the egg that had been displaced about 0.5 m from the nest. Otherwise, there were many instances of eastern chipmunks, eastern cottontails (*Sylvilagus floridanus*), and white-tailed deer (*Odocoileus virginianus*) near whip-poor-will nests and in all these other cases the incubating female remained motionless but alert. Females seemed unbothered by any encounter with birds moving or foraging within 1 m of the nest, including an American Woodcock (*Scolopax minor*), a Common Yellowthroat (*Geothlypis trichas*), several Eastern Towhees (*Pipilo erythrophthalmus*), and several Gray Catbirds (*Dumetella carolinensis*).

Chick period

Behavioral observations during the chick period occurred from hatch until 9 days post-hatch, the latest chicks and adults could be observed with a trail camera before they left the original nest site. Females did not display any noticeable changes in behavior when hatchlings were emerging from their eggs. We observed one female actively remove eggshells by picking them up with her bill and discarding them away from the nest. Female activity while brooding during the day and at night was the same as seen during the incubation period; they regularly shifted their positions, preened, and stretched. Chicks frequently emerged from under the females to defecate a few steps away from their brooding location (always turning away from the nest), and they were observed displaying similar grooming behaviors as the females. We also observed a chick fluttering its gular flap while it was partially exposed to the sun. Adults occasionally moved brooding locations a few steps away and prompted the chicks to join them by vocalizing a soft one-note call sometimes interspersed with grunts (Supplemental Video S8).

All incubation behaviors described above were also observed during the chick period, but provisioning affected the frequency of brooding. Unfortunately, due to issues with the trail camera batteries, we could not quantify behaviors such as brooding and provisioning in the chick period. In general, during this period, females habitually departed at dusk and dawn like they had during incubation, but they also left the nest more regularly at night, returning frequently to the nest to provision the chicks. Males regularly and actively shared in provisioning of chicks in contrast to the incubation period when males were not as engaged. Chicks instigated feeding from the adults by latching onto the adult's bill until they regurgitated food into the chick's mouth (Supplemental Video S9). We observed several instances where males took over brooding the chicks while the female left the nest, similar to what was observed during incubation. We observed one instance of a male continuously brooding chicks from dawn to mid-day. The female returned to the nest mid-day while the male was still brooding, but the pair did not engage in a display before the male left. Males and females often continued their pair-bonding displays when both were present at the nest, but we observed two pairs forego the display and either sit next to each other in silence or make soft one-note vocalizations before one of them left. We did not observe this in any pairs during incubation.

We observed two instances of direct interactions between brooding whip-poor-wills and perceived predators. A brooding male whip-poor-will engaged in the defensive behavior when a northern short-tailed shrew (*Blarnia brevicauda*) came too close (Supplemental Video S10), and a brooding female engaged in active defense (as described above during the snake encounter) against an eastern chipmunk for several minutes (Supplemental Video S11). We also observed several instances where slugs were close to brooding females, but they did not appear to perceive them as threats and did not engage in defensive behaviors as observed previously.

Chick growth trajectories

For all nine growth models, the MCMC trace plots indicated good mixing, posterior predictive check plots showed adequate model fit, and $\widehat{R}$ values were <1.05 confirming model convergence. The most informative measurements of chicks (mean LOO-R^2 estimates ≥0.94) included mass, tarsus length, humerus length, and wing chord (Fig. 2a). Growth curves for the other five measurements are shown in Supplemental Fig. S1. Wing chord, which includes primary feather growth, increased much more quickly than mass and humerus length, and especially tarsus length (Fig. 2a). Both humerus and tarsus length approached asymptotic size by 15 days old whereas at this age both primary feathers and mass were continuing to increase. The timing of maximal growth rates was different for each of the most informative measurements, as were the growth rate trajectories for length of tarsus and humerus and wing chord (Fig. 2b). Wing chord had the longest period of accelerating growth rate, reaching its peak of 6.2 mm/day approximately halfway through the chick growth period

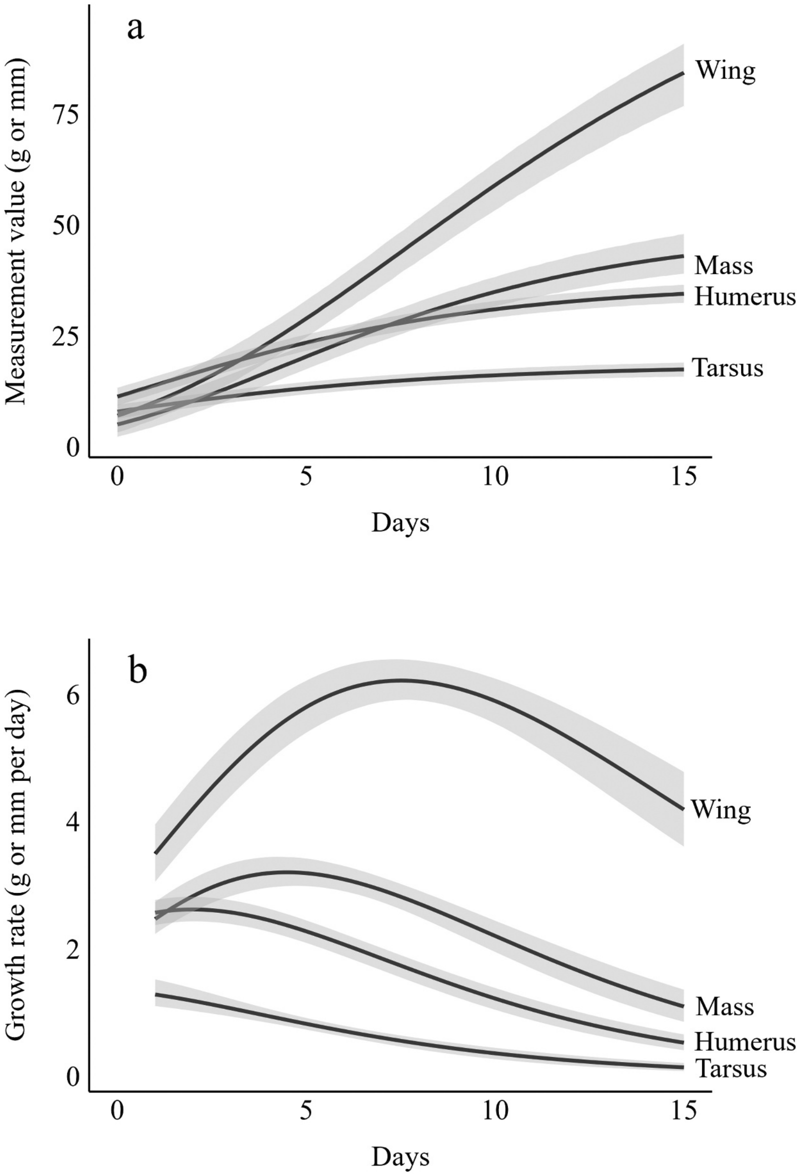

Figure 2. (a) Growth curves with 95% credible intervals (shaded areas) for mass (g), length (mm) of tarsus and humerus, and wing chord (mm) of Eastern Whip-poor-will chicks from hatching to fledging (day 15). These four measurements were the most informative (mean LOO-R^2 estimates ≥ 0.94) of the nine measurements taken (see Supplemental Fig. S1 for growth curves for the other five measurements). (b) Growth rate curves with 95% credible intervals (shaded areas) of Eastern Whip-poor-will chicks from day 1–15 for the four most informative measurements (mean LOO-R^2 estimates ≥ 0.94).

at day 8, and then slowing down more rapidly than any of the other variables. Mass showed a moderate growth rate acceleration for the first 4 days of growth, reaching its maximum of 3.2 g/day at day 5, then steadily declined through the rest of the chick growth period. Humerus length had an initial growth acceleration, reaching its peak of 2.6 mm/day at day

2, but then declined steadily thereafter. The growth rate trajectory for tarsus began at its peak, 1.3 mm/day at day 1, and had a shallow decline throughout the remainder of chick growth.

Predicting chick age

We can now use our growth models to estimate the age of whip-poor-will chicks using the predicted mean size and mass of known-age chicks (Table 1). Chick age is most precisely estimated when all four measurements are available, although age can be estimated with fewer measurements. For example, a chick weighing 33 g would be estimated to be 9–11 days old. However, with an additional measure of wing chord of 64 mm, the same chick would be estimated to be 10–11 days old. Averaging the posterior predictions for the four most informative measurements (Table 1) resulted in age estimate ranges of 1–2 days throughout chick growth.

Discussion

Male and female whip-poor-will behavior during incubation and chick rearing

Some of the behavioral interactions between males and females during incubation and chick rearing that we documented using trail cameras have been anecdotally described in earlier observational studies. Besides a few, brief accounts of male and female whip-poor-will courtship interactions away from the nest (e.g., Bolles 1912; Coale 1920; Tyler 1940; Fuller 1960; Rauth 1979), only Arnold (1937) and Raynor (1941) reported observations (including behavioral interactions) of a few undisturbed males and females at the nest. During incubation, Arnold (1937) described the behavior of a single female as she shifted the eggs and gular fluttered and documented her regular departure from the nest at dusk and dawn for

Table 1. Predictions of chick size (95% credible intervals with mean in parentheses) for each day of Eastern Whip-poor-will chick growth from hatching to fledging (day 15) based on the growth models (see methods for details). The "Combined Value" column represents the averaged predictions of the four individual measurements. See supplemental materials for a datasheet version of the predictive tool and a chick plumage age chart.

Day	Mass	Tarsus Length	Humerus Length	Wing Chord	Combined Value
0	3.0–7.5 (4.9)	6.5–10.7 (8.3)	5.2–11.9 (8.6)	4.5–12.0 (7.1)	5.9–8.9 (7.3)
1	4.9–10.0 (7.2)	8.0–11.9 (9.6)	7.4–14.5 (11.1)	7.1–16.1 (10.3)	8.0–11.4 (9.6)
2	7.3–12.8 (9.9)	9.3–12.9 (10.9)	9.9–17.0 (13.7)	10.5–20.9 (14.1)	10.4–14.2 (12.1)
3	10.0–15.8 (12.8)	10.6–13.9 (12.0)	12.5–19.5 (16.3)	14.6–26.3 (18.7)	13.1–17.2 (14.9)
4	13.0–18.8 (15.9)	11.6–14.7 (13.0)	15.1–21.8 (18.8)	19.3–32.1 (23.8)	16.0–20.3 (17.9)
5	16.2–21.9 (19.1)	12.6–15.4 (13.8)	17.7–23.9 (21.1)	24.6–38.2 (29.4)	19.0–23.4 (20.9)
6	19.3–24.9 (22.3)	13.4–16.0 (14.6)	20.1–25.8 (23.3)	30.3–44.4 (35.3)	22.0–26.5 (23.9)
7	22.3–27.9 (25.3)	14.0–16.5 (15.2)	22.4–27.5 (25.3)	36.3–50.7 (41.5)	25.0–29.4 (26.8)
8	25.1–30.9 (28.1)	14.6–16.9 (15.8)	24.4–29.0 (27.0)	42.4–57.0 (47.7)	27.8–32.2 (29.6)
9	27.7–33.6 (30.6)	15.1–17.3 (16.3)	26.2–30.3 (28.5)	48.5–63.1 (53.8)	30.5–34.9 (32.3)
10	30.0–36.1 (33.0)	15.6–17.6 (16.7)	27.7–31.4 (29.8)	54.5–68.9 (59.8)	33.1–37.3 (34.8)
11	32.1–38.4 (35.0)	15.9–17.9 (17.0)	29.1–32.4 (30.9)	60.2–74.4 (65.5)	35.4–39.6 (37.1)
12	33.8–40.4 (36.8)	16.2–18.1 (17.3)	30.2–33.3 (31.9)	65.6–79.6 (71.0)	37.6–41.6 (39.3)
13	35.2–42.1 (38.4)	16.4–18.4 (17.5)	31.1–34.0 (32.7)	70.7–84.5 (76.1)	39.5–43.5 (41.2)
14	36.4–43.7 (39.8)	16.6–18.6 (17.7)	31.9–34.7 (33.4)	75.4–89.0 (80.9)	41.2–45.2 (42.9)
15	37.4–45.0 (41.0)	16.8–18.7 (17.8)	32.5–35.2 (34.0)	79.7–93.1 (85.2)	42.8–46.8 (44.5)

approximately 15–25 min, only seeing the male at the nest a single time out of the many days they monitored the nest. Raynor (1941) observed a single female leave the nest for 61 min at dusk, for two short durations at night (10 min), and for 15 min at dawn, with the male incubating briefly at dusk and during only one of the nighttime bouts. Kent and Vane (1958), Babcock (1975), and Cink et al. (2020) also reported males incubating eggs. Raynor (1941) directly observed a single male and female nest-associated pair-bonding display whose description is similar to what we observed (including the grunting vocalization) at all 12 nests. In addition, both Arnold (1937) and Raynor (1941) reported the male actively and regularly participating in brooding and feeding chicks, like we reported, and they and Cink et al. (2020) reported the same feeding behaviors we documented with our trail cameras. Cink et al. (2020) also reported the same vocalization adults directed to chicks when moving brooding locations that we observed. In sum, our more extensive observations at 12 nests were consistent with these previous studies but better document the timing and frequency of female incubation recesses, the frequency and duration of male incubation, and the courtship-like behavior of paired males and females while at the nest.

Although several accounts describe courtship displays away from the nest (e.g., Bolles 1912; Coale 1920; Tyler 1940; Fuller 1960; Rauth 1979), descriptions are inconsistent. There are consistent reports of males and females exchanging a guttural grunting vocalization (sometimes referred to as purring or buzzing and described as “gr-gr-gr” or “gaw-gaw-gaw” in the literature). There are also reports on eBird (e.g., Little 1979; Taylor 2020; Anderson 2023; Hershberger 2023) that include recordings of male and female interactions away from the nest which show the same vocalization. These reported vocalizations appear to be the same as observed by Raynor (1941) and what we documented in our trail camera video.

We observed previously undocumented behaviors of females during incubation and between adults and predators. Two previous studies have briefly described females singing and we have documented female whip-poor-wills singing while incubating. Hersey (1923) directly observed a female singing from perches in two different locations and Kent and Vane (1958) described hearing a “softer song” from the direction of the nest they were near that they surmised was the female which seemed to be in response to the male singing from a different location nearby. There is also a recent report from eBird (Watkins 2022) of a female singing from a perch prior to being captured in a mist net. The report by Kent and Vane (1958) is similar to what we observed as the females mostly sang while a male was singing or had just sung close to the nest, but we observed females sing a song as loud as, although shorter than, is typical for males. English et al. (2018), Cink et al. (2020), and Stewart (2023) described snakes, mammalian mesopredators (e.g., raccoons), deer, and arthropods (e.g., ants) as documented predators of whip-poor-will nests, as we also observed. We additionally provide video documentation of gastropods and an arthropod as perceived predators, a slug as a predator of an egg, and an anti-predator defense display, as described above against a snake and chipmunk and shown in supplementary videos in English et al. (2018) against deer. The behavioral interactions between paired males and females, adults and chicks, and adults and predators that we report appear to be similar to those seen in other species of nightjar (e.g., Lack 1932, Eurasian Nightjar *Caprimulgus europaeus*; Vilella 1995, Puerto Rican Nightjar *Antrostomus noctitherus*; Pople 2014, White-winged Nightjar *Eleothreptus candicans*; Jackson

2017, Fiery-necked Nightjar *Caprimulgus pectoralis*; Bodrati and Cockle 2018, Silky-tailed Nightjar *Antrostomus sericocaudatus*).

Growth rates of whip-poor-will chicks and their application for predicting chick age

We provide the first quantitative estimates of growth of Eastern Whip-poor-will chicks. Four measurements (mass, tarsus length, humerus length, and wing chord) were adequate for estimating chick age within 1–2 days up to 15 days old. The development of the predictions of chick size provides a tool to estimate the age of chicks which in turn allows for estimating nest initiation dates, nest hatching dates, and fledging dates without having to monitor nests continuously (see supplemental materials for a datasheet version of the predictive tool and a chick plumage age chart). The ability to estimate these key nesting milestones is essential to determine, for example, how nesting phenology of whip-poor-wills changes across their breeding range, in different quality habitat, and in response to climate change. Other studies have developed similar tools to estimate nestling or chick age of other wild birds based on morphometric measurements (e.g., Ammann 1982; Wails et al. 2014; Sanchez et al. 2021). The best next step is for the predictive tool to be tested with measurements of known-age whip-poor-will chicks from other areas. Fortunately, in the year following this original study, we were able to locate and measure two known-age chicks from a single nest at one of our study sites that had not contributed any chicks to our growth models. The chicks were measured every 2 days from hatching to fledging and the combined measures predictive tool accurately estimated the correct age at every nest visit to the exact day or within a 2 day window that included the correct day. These results are encouraging but need further testing.

An important consideration regarding our growth model parameter estimates is that two of the four most informative measurements, mass and wing chord, did not complete growth prior to fledging. As a result, the estimates for parameter *a* (upper asymptote, estimated adult size) for both mass and wing chord (Supplemental Table S2) are not within one standard deviation of mean adult sizes (mass: 56.0 g, wing chord: 157.0 mm) measured across 46 adult whip-poor-wills captured across all five of our sites and one additional site in 2022 and 2023, but the growth trajectories effectively describe chick growth. Conversely, tarsus length and humerus length completed growth prior to fledging and the estimates for parameter *a* are within one standard deviation of mean adult sizes (18.1 and 35.4 mm) measured across 46 and seven adults, respectively.

Chick growth has been studied in the Fiery-necked Nightjar in Zimbabwe (Jackson 2017) and the Common Pauraque (*Nyctidromus albicollis*) in Venezuela (Verea 2023). Both species are similar in size to the Eastern Whip-poor-will and so Jackson's (2017) and Verea's (2023) measurements of mass, tarsus length, and wing chord of eight chicks and two chicks, respectively, can be directly compared between these three species. Other studies describe chick measurements or growth in other species of nightjar (e.g., Csada and Brigham 1994, Common Poorwill *Phalaenoptilus nuttallii*; Vilella 1995, Puerto Rican Nightjar; Pichorim 2002, Long-trained Nightjar *Macropsalis forcipata*; Luz et al. 2011, Common Pauraque; Kramer and Chalfoun 2012, Common Nighthawk *Chordeiles minor*; Pople 2014, White-winged Nightjar *Eleothreptus candicans*), but the extent of chick measurements are too incomplete to compare to our models of whip-poor-will chick growth. Only Jackson (2017) and Verea (2023) provide daily mean measurements data from which growth rates could be calculated and compared to our results for whip-poor-wills (Table 2). We fit the daily mean measurements provided in Table 1 in Jackson (2017) and Table 1 in Verea (2023) to simple Gompertz growth models using nonlinear least squares regression to generate growth curves and calculate growth rates for direct comparison of growth between the Fiery-necked Nightjar, Common Pauraque, and Eastern Whip-poor-will. If we assume similar extent of credible intervals for Fiery-Necked Nightjars and Common Pauraques as what we predicted for whip-poor-wills, the 95% credible intervals for all three species would overlap, indicating similar growth patterns across the species. We additionally calculated the percentage of adult mass, tarsus length, and wing chord at hatch and at the end of each study period for Eastern Whip-poor-will, Fiery-necked Nightjar, Common Pauraque, Puerto Rican Nightjar, and Long-trained Nightjar chicks using the chick measurements reported in Table 1 in Jackson (2017), Table 1 in Verea (2023), and in the results sections of Vilella (1995) and Pichorim (2002). The percentages of adult sizes at hatch and at the end of each study period were generally consistent across all nightjar species (Table 3). Tarsus length was ~48% adult tarsus length at hatch and reached adult size by the end of the study periods. Mass was ~11% adult mass at hatch and reached ~80% adult mass at the end of the study periods. Wing chord was ~7% adult wing chord at hatch and reached ~55% adult wing chord at the end of the study periods.

Table 2. Comparisons of maximum growth rates, the ages at maximum growth rates, and linear growth rates across 10 species of aerial insectivores.

	Mass (g)		Tarsus Length (mm)		Wing Chord (mm)		
Species	Max Growth Rate (g/day)	Age at Max Growth Rate	Max Growth Rate (mm/day)	Age at Max Growth Rate	Max Growth Rate (mm/day)	Age at Max Growth Rate	Reference[c]
Eastern Whip-poor-will	3.2	5	1.3	1	6.2	8	
Fiery-necked Nightjar[a]	(2.5)	(6)	(0.8)	(1)	(6.3)	(9)	1
Common Pauraque[a]	(3.75)	(4)	(1.23)	(1)	(7.80)	(8)	2
Eastern Kingbird[a]	(3.09)	5.5 (4)	(1.63)	3.5 (2)	(4.24)	9.5 (9)	3
Eastern Phoebe[a]	(1.82)	6.1 (5)	(1.36)	4.5 (3)	(3.92)	10 (9)	3
Fork-tailed Flycatcher[b]	3.27	5.09					4
Scissor-tailed Flycatcher[b]	2.97	5.97					4
	Linear Growth Rate (g/day)		Linear Growth Rate (mm/day)		Linear Growth Rate (mm/day)		
Tree Swallow	2.14		0.96		5.49		5
Barn Swallow	1.96		0.84		5.35		5
Cliff Swallow	2.21		1.08		5.15		5
Eastern Whip-poor-will	2.92		0.83		5.53		
Fiery-necked Nightjar[a]	(2.54)		(0.68)		(5.42)		1
Common Pauraque[a]	(3.21)		(1.08)		(6.53)		2
Eastern Kingbird[a]	(2.80)		(1.27)		(3.74)		3
Eastern Phoebe[a]	(1.69)		(1.22)		(3.43)		3

[a] Maximum growth rates and ages at maximum growth rates were derived by fitting daily mean measurements of Fiery-necked Nightjar (Table 1 in Jackson 2017), Common Pauraque (Table 1 in Verea 2023), and Eastern Kingbird and Eastern Phoebe (Table 1 in Murphy 1981) chicks to simple Gompertz growth models using nonlinear least squares regression. For comparison of the linear growth rates of the swallow species reported in Ramstack et al. (1998), linear growth rates were derived by fitting the daily mean measurements of chicks for all species to linear least squares regression models following the methods in Ramstack et al. (1998). Values not in parentheses are those reported by the authors, values in parentheses are from our estimates.

[b] Maximum growth rates reported in Table 1 in Tuero et al. (2018) were averaged over the 3 years of the study.

[c] 1: Jackson (2017); 2: Verea (2023); 3: Murphy (1981); 4: Tuero et al. (2018); 5: Ramstack et al. (1998).

Table 3. Percent of adult mass, tarsus length, and wing chord of chicks of five nightjar species at hatch and at the end of each study period.

Species	% Adult Mass[a]	% Adult Tarsus Length[a]	% Adult Wing Chord[a]	Reference
Hatch				
Eastern Whip-poor-will	11.6	50.3	6.8	
Fiery-necked Nightjar	10.4	53.6	6.4	Jackson (2017)
Common Pauraque	9.0	40.3		Verea (2023)
Puerto Rican Nightjar	11.6			Vilella (1995)
Long-trained Nightjar	12.0	46.1		Pichorim (2002)
End of Study Period[b]				
Eastern Whip-poor-will	73.0	100	53.7	
Fiery-necked Nightjar	78.0	100	51.9	Jackson (2017)
Common Pauraque	75.4	97.3	61.7	Verea (2023)
Puerto Rican Nightjar	100			Vilella (1995)
Long-trained Nightjar	77.7	100	49.3	Pichorim (2002)

[a] Measurements for Fiery-necked Nightjar and Puerto Rican Nightjar adults taken from their Birds of the World accounts (Fiery-necked Nightjar, Kirwan et al. 2022; Puerto Rican Nightjar, Vilella 2020). Measurements for Common Pauraque adults averaged over five males and five females from the William H. Phelps Ornithological Collection in Caracas, Venezuela. Measurements for Long-trained Nightjar adults taken from Pichorim (2002).

[b] Eastern Whip-poor-will: 15 days; Fiery-necked Nightjar: 20 days; Common Pauraque: 15 days; Puerto Rican Nightjar: 14 days; Long-trained Nightjar: mass 18 days, tarsus 21 days, wing 17 days.

We compared the growth rates of Eastern Whip-poor-will, Fiery-necked Nightjar, and Common Pauraque chicks to that of other species of aerial insectivores (Table 2) including the Eastern Kingbird (*Tyrannus tyrannus*) and Eastern Phoebe (*Sayornis phoebe*) (Murphy 1981), Fork-tailed (*Tyrannus savana*) and Scissor-tailed (*Tyrannus forficatus*) flycatchers (Tuero et al. 2018), and Tree (*Tachycineta bicolor*), Barn (*Hirundo rustica*), and Cliff (*Petrochelidon pyrrhonota*) swallows (Ramstack et al. 1998). We used the same methods described above to fit the daily mean measurement data of Eastern Phoebe and Eastern Kingbird nestlings included in Table 1 in Murphy (1981) to Gompertz growth models, from which we derived growth rate estimates. In order to compare growth rates of Eastern Whip-poor-will, Fiery-neck Nightjar, Common Pauraque, Eastern Kingbird, and Eastern Phoebe chicks to the linear growth rates reported for the swallow species, we fit the daily mean measurements data for all five species to a linear least squares regression model as described in the methods section of Ramstack et al. (1998). Across all species, the growth rate of wing chord was consistently more rapid than mass, while tarsus length was consistently the slowest. Linear and maximum mass growth rates and the ages at which maximum growth was reached appear similar across all species. Likewise, linear and maximum tarsus growth rates were similar across all species, but the age when maximum tarsus growth was reached was later in the Eastern Phoebe and Eastern Kingbird nestlings compared to the nightjar species. Linear and maximum wing growth rates were slowest in both the Eastern Phoebe and Eastern Kingbird nestlings, whereas the three swallow species and three nightjar species showed similar linear growth rates. The lack of information about the variability in growth rates within each species (excluding whip-poor-wills) limits our ability to make more robust interpretations of these data.

Conservation implications and future directions

Our findings that paired males and females regularly interact at the nest during incubation and that males actively participate in chick rearing suggest that management implemented in areas where males are present will benefit both sexes and their nests. The ability to estimate chick age with our predictive tool will enable researchers and managers to estimate whip-poor-will nesting phenology including timing of the nesting stages (e.g., nest initiation, hatch, and fledgling) which will be important for tracking responses to climate change. Additionally, having known ages for nests and nestlings will improve survival analyses by allowing for more precise estimates of age-specific survival rates and identification of critical periods of mortality throughout development. Our growth models also serve as a baseline that can be expanded to examine the effects of habitat quality on growth. Future research should focus on testing the predictive tool against known-age chicks at other locations in the whip-poor-will breeding range, as well as collecting further morphometric data on known-age chicks so that the growth models may be further refined. Additionally, further studies are needed to determine how pairs share in incubation and chick provisioning and how environmental factors such as habitat quality influence parental investment.

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Author contributions

Liam Corcoran: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing- Original Draft, Writing- Review and Editing, Visualization, Supervision, Project administration.
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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

All data and code associated with the analyses in this study are available here: https://github.com/liam-corcoran117/whip-poor-will. All supplementary videos can additionally be found stored at the Macaulay Library here: https://search.macaulaylibrary.org/catalog?taxonCode=easwpw1&regionCode=US-RI&userId=USER853915.

Ethics statement

Research was conducted under the approval of the Institutional Animal Care and Use Committee (IACUC #295926–19) at the University of Rhode Island for permission to use vertebrate animals in research. Additional research permits were obtained from the Rhode Island Division of Fish and Wildlife for a state scientific collector's permit (permit #2023–08-W) and the U.S. Geological Survey Bird Banding Lab for a federal banding permit (permit #22923).

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