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## First demographic estimates for endangered Florida bonneted bats suggest year-round recruitment and low apparent survival

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Estimates of the demographic information necessary to project future population changes are lacking for the endangered Florida bonneted bat (*Eumops floridanus*). We conducted a mark–recapture study on a population of bonneted bats using bat houses on Babcock-Webb Wildlife Management Area, Charlotte County, Florida, United States. We captured 175 individuals during 6 capture events that recurred every 4 months between April 2014 and December 2015. We implanted passive integrated transponder tags in all captured individuals and used open population capture–recapture models to estimate apparent survival, recruitment, and population growth rates of this population. Key model assumptions were evaluated via simulation. Apparent survival estimates were lower than estimates for most other bat species. Juveniles had lower annual apparent survival ( $\varphi = 0.09$  [95% confidence interval [CI]: 0.04–0.19]) than adults ( $\varphi = 0.46$  [0.36–0.57]). Recruitment was constant between sexes and over time ( $f = 0.48$  [0.23–0.75]). Apparent survival had a greater influence on population growth rates than did recruitment, indicating that low survival rates could lead to population declines. Models of population growth rates showed a stable to potentially declining population trend, although the trend was highly variable, with estimates ranging from large declines to increases ( $\lambda = 0.89$  [0.65–1.22]). Any potential declines in the population may be more pronounced in adult females ( $\lambda = 0.81$  [0.58–1.13] compared to  $\lambda = 1.11$  [0.74–1.69] for males); however, the 95% CI of the population growth rate included 1, indicating a need for additional research to derive more precise estimates. This work represents the 1st estimates of demographic parameters of this endangered species.

Key words: conservation, *Eumops floridanus*, Florida, population dynamics, population trend, recruitment, survival

Knowledge of mammalian demographic rates is crucial for management of endangered species. An understanding of survival and recruitment rates can elucidate causes of decline and assist with development of recovery efforts and management plans (Morris and Doak 2002; Bakker et al. 2009). Understanding which demographic rates have the greatest influence on population growth can also provide valuable information on what ecological processes might be limiting recovery of threatened species (Johnson et al. 2010), and are useful for informing management actions that may promote recovery. Unfortunately, estimates of demographic parameters are often difficult to obtain for rare and elusive species (Tear et al. 1995; Fieberg and Ellner 2001).

Over 30% of bats (order Chiroptera) are considered either threatened or data are deficient to determine population

status by the International Union for Conservation of Nature (Timm and Arroyo-Cabrales 2008). Despite the need for understanding basic life history and population parameters for informing research and management needs, relatively few studies have investigated survival and recruitment rates of bats (O’Shea et al. 2004). Compared to other mammals of their size, bats can be characterized as “slow” species along the fast–slow continuum (O’Shea et al. 2004); they are relatively long-lived (Tuttle and Stevenson 1982; Bielby et al. 2007) and have low reproductive outputs (Barclay and Harder 2003). Populations of slow species are expected to be sensitive to fluctuations in adult survival (O’Shea et al. 2004; Pryde et al. 2005; Schorcht et al. 2009) and have relatively high survival rates. For bat species in North America, survival of adults generally ranges from 0.70 to 0.80 (Table 1),

**Table 1.**—Apparent survival estimates of Chiroptera from previous studies. Whenever possible, survival estimates for both males and females are presented. NA (not applicable) indicates that estimates were not reported.

Species	Survival rate			Reference
	Male	Female	Combined	
<i>Chalinolobus tuberculatus</i>	NA	0.590–0.790	NA	Pryde et al. (2005)
<i>Eptesicus fuscus</i>	0.76	0.817	NA	Goehring (1972)
<i>E. fuscus</i>	NA	NA	0.774	Beer (1955)
<i>E. fuscus</i>	0.697 ± 0.061	0.465 ± 0.061	NA	Hitchcock et al. (1984)
<i>Eptesicus serotinus</i>	NA	NA	0.870 ± 0.03	Chauvenet et al. (2014)
<i>E. serotinus</i>	NA	NA	0.810 ± 0.02	Chauvenet et al. (2014)
<i>Macroderma gigas</i>	0.430–0.660	0.570–0.770	NA	Hoyle et al. (2001)
<i>Molossus molossus</i>	NA	NA	0.524 (0.294–0.724)	Gager et al. (2016)
<i>Myotis dasycneme</i>	NA	NA	0.67	Sluiter et al. (1971)
<i>M. dasycneme</i>	NA	NA	0.667	Bezem et al. (1960)
<i>Myotis daubentonii</i>	NA	NA	0.8	Bezem et al. (1960)
<i>Myotis emarginatus</i>	NA	NA	0.701	Bezem et al. (1960)
<i>Myotis leibii</i>	0.757 ± 0.111	0.421 ± 0.071	NA	Hitchcock et al. (1984)
<i>Myotis lucifugus</i>	0.771	0.857	NA	Humphrey and Cope (1976)
<i>M. lucifugus</i>	0.816 ± 0.010	0.708 ± 0.022	NA	Keen and Hitchcock (1980)
<i>M. lucifugus</i>	NA	0.56–0.90	NA	Frick et al. (2010)
<i>Myotis myotis</i>	NA	NA	0.637	Bezem et al. (1960)
<i>Myotis mystacinus</i>	NA	NA	0.752	Bezem et al. (1960)
<i>Myotis sodalis</i>	0.699	0.759	NA	Humphrey and Cope (1977)
<i>M. sodalis</i>	NA	NA	0.642	Boyles et al. (2007)
<i>Perimyotis subflavus</i>	0.57	0.759	NA	Davis (1966)
<i>Pipistrellus pipistrellus</i>	0.44	0.54	NA	Gerell and Lundberg (1990)
<i>Rhinolophus euryale</i>	0.83	NA	NA	Dinale (1968)
<i>Rhinolophus hipposideros</i>	NA	NA	0.567	Bezem et al. (1960)

and there is some evidence that survival of females is higher than that of males (Table 1).

Low reproductive rates and high longevity combined with limited geographic range may make some bat species at higher risk of extinction than other mammals of similar size (Purvis et al. 2000). The Florida bonneted bat (*Eumops floridanus*) is one such species. The Florida bonneted bat (hereafter, bonneted bat) was federally listed as endangered in 2013 and is considered critically endangered by IUCN (Timm and Arroyo-Cabrales 2008; United States Fish and Wildlife Service [USFWS] 2013). Endemic to southern Florida, with an estimated range of approximately 12,000 km<sup>2</sup> or less (Florida Fish and Wildlife Conservation Commission [FWC] 2011; USFWS 2011), the bonneted bat is believed to have one of the most limited geographic ranges of any bat species in North America (Belwood 1992). Although the number of bonneted bats is believed to be small and declining (Timm and Arroyo-Cabrales 2008; USFWS 2013), no actual estimates of demographic parameters exist. This lack of information makes it impossible to understand how potential threats and management activities have affected the population (Romesburg 1981; Campbell et al. 2002).

To increase our understanding of bonneted bat demographic rates and the factors influencing them, we conducted a mark-recapture study of bonneted bats roosting in bat houses on Fred C. Babcock-Cecil M. Webb Wildlife Management Area (BWWMA), Charlotte County, Florida. Our objectives for this study were to 1) estimate rates of apparent survival, recruitment, and population growth; 2) determine if demographic rates were influenced by age and sex of bonneted bats or varied over time; and 3) compare the relative influence of survival and recruitment on the population growth rate of bonneted bats. We

predicted that apparent survival would be higher in females, and apparent survival of juveniles (< 1 year old) would be lower than that of adults, as documented in other species of bats (O'Shea et al. 2004). We also predicted that survival of adults would have a greater effect on population growth rate than recruitment, which is typical of “slow” species.

## MATERIALS AND METHODS

*Study area.*—We conducted all research on BWWMA, a 32,667-ha parcel of land in Charlotte and Lee counties, Florida, United States. BWWMA is owned and managed by the Florida Fish and Wildlife Conservation Commission. The climate is subtropical, with an annual average summer temperature of 27.6°C in July, and average winter temperature of 17.8°C in January (FWC 2003). BWWMA averages 125.3 cm of rainfall annually, with a wet season from July–September and dry season extending through the winter (FWC 2003).

The major natural vegetation communities on BWWMA are dry prairie and hydric pine flatwoods (FWC 2003). The pine-lands of BWWMA are dominated by an open canopy of slash pine (*Pinus elliottii*). They are poorly drained, and on BWWMA remain flooded throughout the wet season (FWC 2003). Around 40% of BWWMA is freshwater marshes, sloughs, and seasonal ponds (FWC 2003). The wildlife management area maintains a short fire return interval, with most areas burned every 2–3 years (FWC 2003). Bonneted bats were first detected in BWWMA in 2006. Wildlife management area staff erected 8 paired 1- or 3-chamber bat houses (Bat Conservation International, Austin, Texas) in 2007–2008. An additional 5 bat houses were erected

in 2012. We conducted our research on all 7 of the paired bat houses used by bonneted bats during our study period.

*Data collection.*—Our mark–recapture study consisted of six 2- to 3-day capture events (CEs) separated by 4 months: 22–25 April 2014, 27–30 August 2014, 15–17 December 2014, 20–24 April 2015, 24–26 August 2015, and 14–16 December 2015. Each bat house was trapped once during each CE; we used stacked mist nets (Avinet, Inc., Dryden, New York) to capture bonneted bats as they emerged from each occupied house. We set up triple-high or double-high mist nets in a triangle or square shape approximately 5 m from each house; houses were completely encircled to minimize chances of bats emerging without being captured. We opened mist nets at sunset, and kept the nets open for a maximum of 3 h. The nets were monitored continuously; when a bat was captured, it was carefully removed from the net and placed in a cotton bag.

We determined sex, age (adult or juvenile), reproductive status, body mass, and forearm length of each bat. Juveniles were distinguished by the partial or complete fusing of phalangeal cartilage or the status of the genitals and mammae (Davis and Hitchcock 1965). We marked each bat with a 12.1 mm, 134.2 kHz FDXB passive integrated transponder (PIT) tag (Biomark Inc., Boise, Idaho). During the first 2 CEs, we sterilized all tags using 70% ethanol before insertion into the lower lumbar region (F. Ridgeley, DVM [Miami Zoo], pers. comm.). In later capture sessions, we used PIT tags that were pre-sterilized and pre-loaded into individual needles. Prior to insertion of each PIT tag, the desired injection site was swabbed with Chlorhexidine solution. After injection, the entry site was sealed with a small amount of Skin Bond (Montreal Ostomy, St. Louis, Missouri). After the tag was inserted, the bats were scanned with a PIT tag reader (Biomark 601 Reader or Biomark Pocket Reader; Biomark, Inc.) to ensure that the PIT tag was properly implanted. During the initial CE in April 2014, every captured bonneted bat had a PIT tag implanted. During subsequent recapture events, all captured bats were scanned with a PIT tag reader and any unmarked individuals had a PIT tag inserted using the above methods. Once processing was complete, bats were released at the capture location. All capture and handling of animals was conducted in accordance with the guidelines for use of mammals in research set forth by the American Society of Mammalogists (Sikes et al. 2011) and all methods were approved by the Institutional Animal Care and Use Committee at the University of Florida (#201308070). We obtained sampling permits from United States Fish and Wildlife Service (#TE 23583B-0) and Florida Fish and Wildlife Conservation Commission (#SUO-49616).

*Assessing model robustness to key assumptions.*—We used Pradel's temporal symmetry framework to develop estimates of detection probability ( $p$ ), apparent survival ( $\varphi$ ; includes both survival and emigration), recruitment ( $f$ ), and population growth rate ( $\lambda$ ) (Pradel 1996; Hines and Nichols 2002). This model is part of the larger “open” class of capture–recapture models and assumes that the population was open to changes from births, deaths, emigration, and immigration. Other key assumptions include 100% tag retention and complete mixing

between marked and unmarked animals (Williams et al. 2002). Because of concerns that tag loss may be occurring in bonneted bats and, if so, uncertainty as to how this tag loss would affect demographic parameter estimates of interest (particularly survival), we first used a simulation framework to assess the influence of variable rates of tag loss and survival on our results. We used GENCAPH1 (J. E. Hines, USGS Patuxent Wildlife Research Center, <http://www.mbr-pwrc.usgs.gov/software.html>) to generate capture histories that mimicked our field sampling design and basic life history information ( $\varphi = 0.70$ ,  $p = 0.60$ , and  $\lambda = 1.25$ ). We then applied tag retention rates (1-tag loss) of 0.90 and 0.50 between each CE.

Because estimates of survival can be confounded with low capture probabilities, we also evaluated model performance with varying survival rates to assess the performance of Pradel's model given the capture probabilities we observed for bonneted bats. We again used GENCAPH1 to generate capture histories at high (0.90), medium (0.70), low (0.50), and very low (0.30) levels of apparent survival. We held detection probability constant at 0.60, tag retention constant at 1.0, and population growth rate at 1.25. We generated capture histories for 6 different CEs. For both the tag retention and survival variation simulations, we then fit these data to Pradel's model in Program MARK version 3.0.3 (White and Burnham 1999) and evaluated model performance by comparing parameter estimates to true values used to generate each data set.

*Data analysis.*—We performed all analyses on the population of bats using the bat houses on BWWMA using Program MARK version 3.0.3 (White and Burnham 1999). We used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) to compare and select models. Models with the lowest  $AIC_c$  value were considered the most parsimonious, while models with an  $AIC_c$  within 2 of the most parsimonious model were considered competing models. We reported all results as rates between CEs (4-month vital rates), unless otherwise specified. We also calculated annual apparent survival to compare rates to other bat populations.

We sequentially fit models from simplest to more complex and evaluated the influence of sex, age, and time on key demographic parameters of interest ( $\varphi$  and  $\lambda$ ) (McCleery et al. 2013). For example, we fixed apparent survival and population growth rate to constant ( $\varphi[.] \lambda[.]$ ) to examine the effects of sex, age, and time between CEs on probability of detection. We then fixed capture probability based on the most parsimonious model identified above, and fixed population growth rate as a constant. To determine the factors influencing apparent survival, we allowed apparent survival to vary as a function of CE, sex, and age and selected the most parsimonious model (holding  $p$  and  $\lambda$  constant). Finally, we fixed capture probability and apparent survival based on the estimates from the most parsimonious models identified previously and allowed population growth rate to vary by CE and sex.

After developing estimates of apparent survival, population growth, and capture probability, we used an alternative parameterization of the Pradel model to estimate recruitment over time (Pradel 1996). We fixed apparent survival and capture



probability to the models that were identified as most parsimonious above, and recruitment was allowed to vary by CE and sex. Pradel's model framework does not allow for the transition of juveniles to adults within the model (White and Burnham 1999), so we did not investigate age effects for population growth rate or recruitment.

## RESULTS

**Simulations.**—High tag loss could lead to a severe underestimation of apparent survival probabilities (Supplementary Data SD1). When we simulated that one-half of the tags were lost between capture intervals, apparent survival was estimated to be 0.32 (0.21–0.44), compared to the actual apparent survival of 0.70. When 90% of the tags were retained between CEs, the estimated apparent survival was very close to the actual value (estimated  $\varphi = 0.73$  [0.63–0.81]). In contrast, population growth rate was relatively robust to variations in tag retention, with a predicted growth rate of 1.22 (1.12–1.32) when tag retention was 90% and a predicted growth rate of 1.22 (1.12–1.33) when tag retention was 50% (compared to the actual  $\lambda$  of 1.25).

The estimated apparent survival probabilities were very close to the actual survival probabilities (Supplementary Data SD1). Low rates of apparent survival led to an underestimation of population growth rate (estimated  $\lambda = 1.08$  [0.97–1.20] when  $\varphi = 0.30$ ). When apparent survival was set to 0.70, which was similar to rates observed in this study (see below), the population growth rate was slightly underestimated ( $\lambda = 1.19$  [1.10–1.29]).

**Mark–recapture study.**—We captured a total of 175 individual bonneted bats during 6 capture sessions; 139 bats were recaptured at least once (Supplementary Data SD2). The most parsimonious model for capture probability included temporal and age effects, with juveniles having a lower probability of capture than adults (Supplementary Data SD3). The lowest overall capture probability occurred in December 2014 ( $p = 0.59$  [95% confidence interval [CI]: 0.44–0.72] for adults,  $p = 0.34$  [0.13–0.63] for juveniles) (Supplementary Data SD3). Capture probabilities for the 1st and last CEs were confounded (White and Burnham 1999). No juveniles were captured in April 2014, confounding the estimate for capture probability of juveniles in the following CE (August 2014).

The most parsimonious model for apparent survival included additive temporal and age effects (Table 2). Overall, apparent survival of adults between CEs ( $\varphi = 0.77$  [0.71–0.83]) was higher than apparent survival of juveniles ( $\varphi = 0.45$  [0.34–0.58]) (Fig. 1). The annual apparent survival for adults was 0.46 (0.36–0.57), whereas the annual apparent survival for juveniles was 0.09 (0.04–0.19). Adults had the highest apparent survival rates between April and August 2015 ( $\varphi = 0.86$  [0.69–0.95]); interestingly, they had the lowest between April and August 2014 ( $\varphi = 0.69$  [0.53–0.82]). Apparent survival of juveniles approached 1.00 between August and December 2014 but was low (around 0.16) between the other CEs (Fig. 1). Lowest overall apparent survival was between December and April 2015 ( $\varphi = 0.70$  [0.53–0.83]) (Fig. 1). There was also some support

for the model including age and sex effects (Table 2), providing evidence that age and sex also account for some variation in apparent survival rates. This model estimated that adult females had the highest apparent survival ( $\varphi = 0.79$  [0.73–0.84]), followed by adult males ( $\varphi = 0.68$  [0.55–0.79]), juvenile females ( $\varphi = 0.53$  [0.36–0.69]), and juvenile males with the lowest ( $\varphi = 0.38$  [0.23–0.56]).

The model for population growth rate that received the most support included an effect of sex, but there was no evidence of temporal variation (Table 2). This suggests that population growth between CEs was 0.93 (0.84–1.04) for females and 1.04 (0.90–1.19) for males, which corresponded to an annual growth rate of 0.81 (0.58–1.13) for females and 1.11 (0.74–1.69) for males (Supplementary Data SD4). Overall, this population of bonneted bats showed a highly variable trend with estimates ranging from large declines (annual  $\lambda = 0.65$ ) to increases (annual  $\lambda = 1.22$ ).

The constant model for recruitment received the most support of all models investigated (Table 2). The annual recruitment estimates according to this model were 0.48 (0.23–0.75) new animals per individual in the population. The proportional contribution of apparent survival on population growth rate was larger than the proportional contribution of recruitment on population growth rate (Supplementary Data SD5).

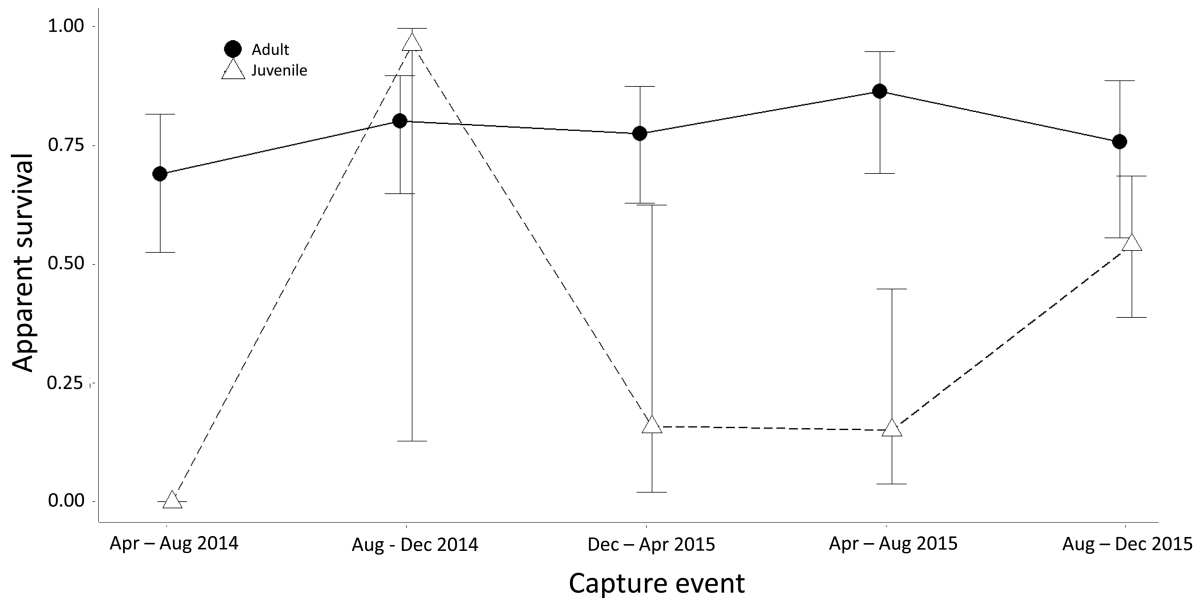
## DISCUSSION

Bonneted bats using the bat houses on BWWMA had lower apparent survival rates than those reported for other species of bats in the western hemisphere (Table 1). Bonneted bats do not hibernate, whereas the majority of demographic studies have been conducted on hibernating bats. The costs associated with not hibernating may contribute to the low apparent survival rates we observed. Turbill et al. (2011) found that annual apparent survival of hibernating species was 15% higher than non-hibernating species of similar body sizes. Non-hibernating bats are believed to face increased risk of mortality throughout the year, both from predation and increased risk of starvation from unpredictable food availability (Wilkinson and South 2002). A demographic study on another molossid that does not hibernate, *Molossus molossus*, also found relatively low apparent survival rates. Monthly survival was  $\approx 0.95$  (Gager et al. 2016), with an extrapolated annual survival  $\approx 0.54$ , similar to the 0.46 (0.36–0.57) apparent survival rate estimated in our study. Apparent survival for bonneted bats was near its lowest levels around the winter months.

Low annual survival rates and the depressed apparent survival rates observed in winter may also be a function of potential edge-of-range effects. Babcock-Webb is located near the northern periphery of the range of the bonneted bat. Additionally, the Florida bonneted bat was considered a subspecies of *Eumops glaucinus* until 2004, when it received species status based on morphology (Timm and Genoways 2004). Recent genetic evidence suggests that species status may not have been warranted (Bartlett et al. 2013); thus, the Florida bonneted bat may be located at the northern edge of

**Table 2.**—Model comparisons of number of parameters (K), AIC<sub>c</sub> values, difference in AIC<sub>c</sub> from the selected model ( $\Delta$ AIC<sub>c</sub>), and model weight (weight) for capture probability (*p*), apparent survival ( $\varphi$ ), population growth rate ( $\lambda$ ), and recruitment (*f*) for Florida bonneted bats (*Eumops floridanus*) occupying bat houses on Babcock-Webb Wildlife Management Area, Charlotte County, Florida from April 2014 to December 2015. AIC<sub>c</sub> = Akaike’s Information Criterion corrected for small sample size; CE = capture event.

Models	K	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Weight
<b>Capture probability (<i>p</i>)</b>				
$\varphi(\cdot) p(\text{CE} + \text{age}) \lambda(\cdot)$	12	1047.97	0.00	0.68
$\varphi(\cdot) p(\text{CE} + \text{age} + \text{sex}) \lambda(\cdot)$	23	1049.43	1.46	0.33
$\varphi(\cdot) p(\text{age} + \text{sex}) \lambda(\cdot)$	6	1111.40	63.43	0.00
$\varphi(\cdot) p(\text{age}) \lambda(\cdot)$	4	1113.13	65.16	0.00
$\varphi(\cdot) p(\text{CE} + \text{sex}) \lambda(\cdot)$	13	1113.87	65.90	0.00
$\varphi(\cdot) p(\text{sex}) \lambda(\cdot)$	4	1118.51	70.54	0.00
$\varphi(\cdot) p(\text{CE}) \lambda(\cdot)$	8	1124.37	76.40	0.00
$\varphi(\cdot) p(\cdot) \lambda(\cdot)$	3	1125.23	77.26	0.00
<b>Survival rate (<math>\varphi</math>)</b>				
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) \lambda(\cdot)$	22	1027.90	0.00	0.74
$\varphi(\text{age} + \text{sex}) P(\text{CE} + \text{age}) \lambda(\cdot)$	17	1030.67	2.77	0.18
$\varphi(\text{age}) P(\text{CE} + \text{age}) \lambda(\cdot)$	15	1033.59	5.69	0.04
$\varphi(\text{CE} + \text{age} + \text{sex}) P(\text{CE} + \text{age}) \lambda(\cdot)$	31	1033.85	5.95	0.04
$\varphi(\text{sex}) P(\text{CE} + \text{age}) \lambda(\cdot)$	15	1046.43	18.53	0.01
$\varphi(\cdot) P(\text{CE} + \text{age}) \lambda(\cdot)$	14	1047.97	20.08	0.00
$\varphi(\text{CE} + \text{sex}) P(\text{CE} + \text{age}) \lambda(\cdot)$	23	1054.70	26.80	0.00
$\varphi(\text{CE}) P(\text{CE} + \text{age}) \lambda(\cdot)$	18	1055.36	27.46	0.00
<b>Population growth rate (<math>\lambda</math>)</b>				
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) \lambda(\text{sex})$	19	1027.04	0.00	0.59
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) \lambda(\cdot)$	18	1027.90	0.86	0.38
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) \lambda(\text{CE})$	21	1032.50	5.46	0.04
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) \lambda(\text{CE} + \text{sex})$	26	1037.35	10.31	0.01
<b>Recruitment (<i>f</i>)</b>				
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) f(\cdot)$	18	1044.53	0.00	0.52
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) f(\text{sex})$	19	1045.50	0.97	0.32
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) f(\text{CE})$	20	1046.92	2.39	0.16
$\varphi(\text{CE} + \text{age}) P(\text{CE} + \text{age}) f(\text{CE} + \text{sex})$	25	1054.55	10.02	0.00



**Fig. 1.**—Apparent survival rates of Florida bonneted bats (*Eumops floridanus*) between 4-month capture intervals in Babcock-Webb Wildlife Management Area, Charlotte County, Florida. The intervals represent April–August 2014, August–December 2014, December 2014–April 2015, April–August 2015, and August–December 2015.

an even larger, Neotropical range (Best et al. 1997; Timm and Arroyo-Cabrales 2008). The depressed winter survival that we observed could be related to cold-intolerance in a tropical species. Anecdotal evidence suggests that bonneted bats are

sensitive to cold. In 2010, a cold spell resulted in the permanent disappearance and presumed mortality of one-half of the bonneted bats using a bat house in North Fort Myers, Lee County (USFWS 2013). To our knowledge, similar mortality events

have not occurred farther south in Florida. There is some support for a link between fitness of vertebrates and the location within a distribution; a meta-analysis by [Sexton et al. \(2009\)](#) found 64 of 112 papers showed reduced fitness of populations at the edge of their ranges.

One limitation of many capture–recapture models is that without estimates of emigration, it is impossible to separate true from apparent survival. For endangered species of conservation concern such as bonneted bats, estimates of true survival are likely of key management interest as management actions could be directed at increasing survival rates to promote recovery. This study was not designed to estimate emigration. However, high site fidelity has been documented for many species of bats ([Lewis 1995](#)), and research on the related *M. molossus* found high site fidelity, particularly for adult females ([Gager et al. 2016](#)). If bonneted bats also demonstrate high roost fidelity, our apparent survival estimates are likely close to true survival estimates. We did observe some evidence that suggests bats may be dispersing, at least temporarily, from bat houses. Fifteen bats (~9% of individuals captured and tagged) were not captured during at least 1 capture period but were recaptured in subsequent sampling events. Seven of these (4% of individuals tagged) were absent for at least 2 consecutive periods before being recaptured, and 1 was absent for 3 consecutive periods before being recaptured. This type of “temporary” emigration has been assessed for other types of capture–recapture models ([Kendall et al. 1995](#)) and with the Pradel models temporary emigration likely leads to lower estimates of detection probability ([Pradel 1996](#); [Pradel et al. 1997](#)). Further assessment of whether or not dispersal is occurring or whether these temporary emigration events may represent other behavioral characteristics such as use of multiple roost sites is an area of future work.

The variation in survival between juvenile and adult bonneted bats using the bat houses on BWWMA provides further evidence that dispersal may be occurring. Decreased survival rates of juveniles less than 1 year of age has been observed for many species of bats (reviewed by [O’Shea 2004](#)); however, there were several signs that suggested that some level of juvenile dispersal was occurring. We observed a clear decline in apparent survival of juveniles in late winter–early spring, indicating that juveniles may be dispersing during the peak reproductive season observed in April. Throughout the study, no juveniles were recaptured in their natal roosts after 8 months ([Ober et al. 2016](#)). It is possible that the low survival rate of juveniles was a combination of high mortality of both sexes and dispersal of males, a pattern that is relatively common in mammals ([Dobson 1982](#)). Bonneted bats have a harem social structure ([Ober et al. 2016](#)); the dispersal of juvenile males could reduce mate competition with the dominant adult male ([Moore and Ali 1984](#)). An alternative hypothesis is that juveniles of both sexes are dispersing from their natal roosts. Dispersal of juvenile females is rare in mammals but has been documented in several species of tropical bats, including *M. molossus*, which has a social structure similar to that of bonneted bats ([McCracken 2010](#); [Nagy et al. 2013](#); [Gager et al. 2016](#)). The fact that survival of juveniles of both sexes declined rapidly over 1 time period provides support for this potential explanation.

This study supports anecdotal evidence suggesting that bonneted bats have an extended breeding season, with juveniles present during every CE with the exception of April 2014. In addition, emergence counts from May to December 2014 documented non-volant young in houses during every month ([Ober et al. 2016](#)). Similarly, reproductive activity has been documented throughout most of the year in the closely related *E. glaucinus* ([Best et al. 1997](#)). Nevertheless, there appeared to be times with more pronounced reproductive activity: during April 2014 and April 2015, nearly all adult female bonneted bats captured were pregnant. Despite this, we never observed a subsequent increase in the number of juveniles. Our inability to detect an increase in the abundance of juveniles may be because our capture intervals were too far apart, leading to missed trends in recruitment. [Gager et al. \(2016\)](#) documented a similar trend in reproduction in *M. molossus* in Panama, with a peak in pregnancies occurring in April. They monitored a subset of juveniles that were tagged in July and September of that year; the juveniles all disappeared from the roost between July of that year and February of the next year ([Gager et al. 2016](#)). With the low apparent survival rates documented for juveniles during this study, it is likely that a number of juveniles born soon after the April capture session would either have died or dispersed from their natal roosts before our August CE. More frequent captures will be necessary to document these finer-scale trends in recruitment.

Our study suggests that the population of bonneted bats using the bat houses on BWWMA has a stable to slightly declining trend. Somewhat concerning is the apparent loss of adult females from the population. Although the *CIs* of female population growth crossed 1.00 (indicating a stable population), our results suggest that the population of female bonneted bats using bat houses on BWWMA may be declining. Overall population growth was driven by survival of adults, which was expected based on previous demographic studies of bats ([O’Shea et al. 2004](#)). Although adult females had the highest survival rates, this population was also heavily female-biased ([Ober et al. 2016](#)). The low apparent survival of females may limit population growth and reduce recruitment. Combined, these patterns may be detrimental to this population of endangered bonneted bats.

It is important to take the assumptions of Pradel’s model into consideration when interpreting our results. [Hines and Nichols \(2002\)](#) found that trap response of individuals led to a substantial bias in the estimation of population growth rate. We did not witness evidence of trap response during our study; although bats occasionally did not emerge from the bat house, the number of individuals observed in the houses after nets were closed appeared to vary randomly throughout the study. Even if a trap response occurred, or individuals had heterogeneous capture probabilities, [Hines and Nichols \(2002\)](#) recommend using only models that do not look at time effects on population growth. Our selected models did not include an effect of time on growth rate, making our estimates relatively robust to biases from heterogeneous capture probabilities or a trap response ([Hines and Nichols 2002](#)). Deaths during capture were also found to lead to a biased estimation of population growth rate ([Hines and Nichols 2002](#)).

Again, we had no indication that there was any trap- or tag-related mortality of captured animals. The major assumption that was likely violated during our study was that marks were not lost. We chose to mark all bats with PIT tags because of high retention rates observed in other studies (Ellison et al. 2007). However, 11 PIT tags were recovered underneath the occupied bat houses between April 2014 and April 2016. The actual number of lost PIT tags is unknown, as it is probable that bats also lost PIT tags when foraging away from the bat houses. It is unknown if bats that lost PIT tags were recaptured after the tag was lost and marked as new individuals. Our simulations showed that population growth rate estimates were relatively robust to high levels of tag loss, indicating that this assumption violation may not have resulted in substantial bias to our estimate of population growth rate.

This study represents the 1st estimates of demographic parameters of the federally endangered Florida bonneted bat and has important conservation implications. Our results suggest that low survival rates for this species could lead to population declines. We can use these results as a target while developing conservation and recovery plans for this endangered species. While this study provides a baseline of demographic information, it also highlights the need for further research. Additional research focused on demographics of bats using natural structures as roosts, on bats throughout the range of the species, and on the dispersal of individuals will be critical to elucidate whether the apparent survival rates are low due to mortality or because bats are using roosts that we are not yet aware of. If the latter is the case, the conservation of these roosts will be crucial for the survival and recovery of this population. Future research should focus on how many roosts are necessary to sustain a population of bonneted bats, and whether the demographic trends observed in this study are consistent throughout the range of the bonneted bat and between natural and artificial roosts.

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#### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Results of simulations of demographic parameters of Florida bonneted bats when a) tag retention = 0.90 between capture events, b) tag retention = 0.50 between capture events, c) survival ( $\varphi$ ) = 0.90 between capture

events, d) survival ( $\varphi$ ) = 0.70 between capture events, and e) survival ( $\varphi$ ) = 0.50 between capture events.

**Supplementary Data SD2.**—Number of Florida bonneted bats (*Eumops floridanus*) captured from occupied bat houses on Babcock-Webb Wildlife Management Area, Charlotte County, Florida at each of 6 capture events during a demographic study from April 2014 to December 2015.

**Supplementary Data SD3.**—Capture probabilities ( $p$ ) of adult and juvenile Florida bonneted bats (*Eumops floridanus*) captured from occupied bat houses on Babcock-Webb Wildlife Management Area, Charlotte County, Florida during a demographic study from April 2014 to December 2015. Estimates from the 1st and last capture events were confounded and not included.

**Supplementary Data SD4.**—Average annual growth rate ( $\lambda$ ) estimates for male and female Florida bonneted bats (*Eumops floridanus*) using bat houses on Babcock-Webb Wildlife Management Area, Charlotte County, Florida. Estimates are the results of a demographic study that took place from April 2014 to December 2015.

**Supplementary Data SD5.**—Relationship between adult survival ( $\hat{\varphi}$ ) and recruitment ( $\hat{f}$ ) on derived population growth ( $\hat{\lambda}$ ) of Florida bonneted bats (*Eumops floridanus*) using bat houses on Babcock-Webb Wildlife Management Area, Charlotte County, Florida from April 2014 to December 2015.

$\frac{\hat{\varphi}}{\hat{\lambda}}$  represents influence of adult survival on population growth rate, while  $\frac{\hat{f}}{\hat{\lambda}}$  represents the influence of recruitment on population growth rate.

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