

Life histories and conservation of long-lived reptiles, an illustration with the American crocodile (*Crocodylus acutus*)

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Abstract

1. Successful species conservation is dependent on adequate estimates of population dynamics, but age-specific demographics are generally lacking for many long-lived iteroparous species such as large reptiles. Accurate demographic information allows estimation of population growth rate, as well as projection of future population sizes and quantitative analyses of fitness trade-offs involved in the evolution of life-history strategies.
2. Here, a long-term capture–recapture study was conducted from 1978 to 2014 on the American crocodile (*Crocodylus acutus*) in southern Florida. Over the study period, 7,427 hatchlings were marked and 380 individuals were recaptured for as many as 25 years. We estimated survival to be strongly age dependent with hatchlings having the lowest survival rates (16%) but increasing to nearly 90% at adulthood based on mark–recapture models. More than 5% of the female population were predicted to be reproductive by age 8 years; the age-specific proportion of reproductive females steadily increased until age 18 when more than 95% of females were predicted to be reproductive. Population growth rate, estimated from a Leslie–Lefkovich stage-class model, showed a positive annual growth rate of 4% over the study period.
3. Using a prospective sensitivity analysis, we revealed that the adult stage, as expected, was the most critical stage for population growth rate; however, the survival of younger crocodiles before they became reproductive also had a surprisingly high elasticity. We found that variation in age-specific fecundity has very limited impact on population growth rate in American crocodiles.
4. We used a comparative approach to show that the original life-history strategy of American crocodiles is actually shared by other large, long-lived reptiles: while adult survival rates always have a large impact on population growth, this decreases with declining increasing growth rates, in favour of a higher elasticity of the juvenile stage.
5. Crocodiles, as a long-lived and highly fecund species, deviate from the usual association of life histories of “slow” species. Current management practices are focused on nests and hatchling survival; however, protection efforts that extend to juvenile crocodiles would be most effective for conservation of the species, especially in an ever-developing landscape.

KEYWORDS

capture–mark–recapture, crocodylian, demography, population dynamics, sensitivity analysis

1 | INTRODUCTION

Population growth (λ) plays a central role in conservation and management of species (Sibley, Hone, & Clutton-Brock, 2003), and understanding its environmental and anthropogenic determinants are at the core of what ecologists set out to explain (Coulson, Gaillard, & Festa-Bianchet, 2005). In practice, the conservation status and viability of populations (Shaffer, 1990), consequences of epizootics (Lachish, Jones, & McCallum, 2007) or impact of human activities (Bieber & Ruf, 2005; Moloney, Cooper, Ryan, & Roy Siegfried, 1994) are all ultimately determined by population growth. Demographic rates (reproduction, survival, immigration and emigration rates) and any changes therein contribute to variation in population abundance and thereby a change in λ . Changes in λ can be the result of a change in actual demographic rate, correlation with other values, temporal variability, and sensitivity of population growth rate to demographic parameters themselves (Haridas & Tuljapurkar, 2005). Sensitivity, or perturbation analyses, quantifies the response of population growth rate to changes in demographic rates and indicates what may have the greatest effect on λ (Caswell, 2000). Increases in human population size and associated habitat degradation have caused numerous species declines, and knowledge about a species response to variation in demographic parameters is crucial for species survival. Determining how a species responds to environmental variability at the population level provides information on how to allocate resources (Salomon, McCarthy, Taylor, & Wintle, 2013) and to focus management and conservation policies on the most important stage of a species' life cycle to ensure population viability (Caswell, 2000; Heppell, Caswell, & Crowder, 2000).

Both a species' life cycle and its life-history strategy will define how sensitive population growth rate is to different demographic rates. Demography theory established, in a simple two-age class model, that sensitivity of population growth rate to survival and reproductive rates is a direct function of the species' generation time (*sensu* Leslie, 1966). Longer generation time equates with greater sensitivity of λ to survival rate of the adult age class (Lebreton & Clobert, 1991). Moreover, generation time organizes vertebrates along a "slow–fast" continuum (Gaillard et al., 2005) with co-variation of life-history traits and body size (Pontier et al., 1989), ranging from "fast" species that are small in size, mature quickly, have high fecundity, but have low adult survival (e.g., passerines, Sæther & Bakke, 2000; and small mammals Oli & Dobson, 1999) to slow species that are generally large in size, with delayed maturity, and low fecundity, but have high adult survival (e.g., large herbivores, Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000 and marine mammals Frie, Stenson, & Haug, 2012). Depending where a species lies along this continuum will affect its population age structure and how λ will respond to changes in demographic traits (Beckerman, Benton, Ranta, Kaitala, & Lundberg, 2002). Generally in

fast species, λ has been shown to have a high sensitivity to fecundity and juvenile survival (Pfister, 1998), whereas in slow species, λ is more sensitive to adult survival rates and less so to reproductive rates (Gaillard & Yoccoz, 2003).

The case of large, long-lived reptiles presents a conundrum because they display life-history traits of both slow and fast species, combining high adult survival with large fecundity and low juvenile survival. Despite limited demographic data on crocodylians, this taxon seems to have different life-history strategies compared with similar-sized homeotherms (Wilkinson & Rhodes, 1997). Crocodylians include crocodiles, alligators, caimans and gharials (Grigg & Kirschner, 2015), and they are long-lived reptiles with marked delayed sexual maturity but exhibit iteroparous reproduction and high fecundity (Kushlan & Mazzotti, 1989). Reports exist of very large, hence supposedly very old, crocodiles in the wild (Webb, Messel, Crawford, & Yerbury, 1978; Woodward, White, & Linda, 1995), but data on age-specific survival rates of wild crocodylians are very limited (Lance, 2003). Hatchling and juvenile periods are generally thought to have lower rates of survival relative to adults (Mazzotti, 1983; Pike, Pizzatto, Pike, & Shine, 2008), and few reliable estimates of age-based survivorship exist in crocodiles, thus making demographic synthesis less than accurate.

The particular life-history strategies of large reptiles may lead to different sensitivity patterns of λ to variation in demographic traits (i.e., age at maturity, mean annual fecundity and annual survival) than what is usually reported for long-lived species, and would require us to adapt conservation strategies that are suitable for long-lived reptiles (Crouse, Crowder, & Caswell, 1987). Moreover, the sensitivity of population growth rate to variation in demographic traits in crocodylians is typically explored using stage-based population projection matrix models (Richards, 2003; Webb et al., 1978), because age-specific demographic data are difficult to obtain and because life-history traits are tightly associated with size/stage in these species. In this study, however, we go beyond common limitations and use long-term individual-based data for known-aged crocodiles, as a model species of long-lived reptiles, to build a population projection matrix model and to compare our results with size- or stage-based demography.

The American crocodile is a federally threatened species in the United States and has experienced severe declines due to overexploitation and loss of habitat for nesting throughout its historical range (Thorbjarnarson, 2010). In the southern United States, the species may be affected by ecosystem restoration projects in the Greater Everglades (Mazzotti et al., 2009) and could benefit from management strategies that implement effective demographic tools that can also be useful for ecological comparisons. In this article, we use a long-term capture–recapture study of 35+ years of monitoring American crocodiles (*Crocodylus acutus*) at the margin of their northernmost distribution in south Florida, to assess and understand crocodylian

demography, estimate population growth rate and outline the species conservation status. We set out to assess how life-history strategy affects sensitivity of population growth rates to demographic rates of the American crocodile.

We tested the hypotheses that (1) survival rates are lowest for younger American crocodiles (Magnusson, 1982), and (2) population growth rate of a long-lived species, that can live at least 25 years (this study), is most sensitive to variation in adult survival rate than to variation in recruitment parameters (Pfister, 1998). We predicted high adult survival and high relative sensitivity of λ to variation in adult survival. Because of a large clutch size and expected low hatchling and juvenile survival (Kushlan & Mazzotti, 1989), fecundity should not be as critical to population dynamics as adult survival, and thus, we also predicted that relative sensitivity of λ to fecundity would be low. We present our case study on American crocodiles, a model species representative of long-lived reptiles, to assess their position along the slow-fast continuum and later place our findings in context with other large, long-lived reptiles to assess the generality of our findings.

2 | MATERIALS AND METHODS

2.1 | Study species

The American crocodile is the most widely distributed species of New World crocodiles (IUCN, 2012) occurring from south Florida and coastal Mexico down into South America and along the Caribbean (Ponce-Campos, Thorbjarnarson, & Velasco, 2012). The species is presently classified as Vulnerable on IUCN Red List (Ponce-Campos et al., 2012) and is on Appendix I of CITES. In southern Florida, *C. acutus* nesting was restricted to a small area of northeastern Florida Bay in Everglades National Park and northern Key Largo by the early 1970s (Kushlan & Mazzotti, 1989). The species was placed on the Federal Endangered species list in 1975 (Federal Register 40), but with critical monitoring and management efforts (Brandt et al., 1995; Mazzotti, Brandt, Moler, & Cherkiss, 2007), the Florida population of *C. acutus* was reclassified from endangered to threatened in 2007 (Federal Register 72).

2.2 | Study area

The study site is at the Turkey Point power plant (TP) owned by Florida Power and Light Co., which is located in southeastern Miami-Dade county, Florida (25°26'6.96"N, 80°19'52.95"W). TP is bordered by Biscayne National Park to the east and Card Sound to the south and is within Federally designated critical crocodile habitat (Figure 1). The 2,388 ha site consists of a closed-loop series of 60-m wide cooling canals separated by 40-m wide earthen berms and serves to circulate water to cool the plant's condensers (Figure 1). Turkey Point has served as an important source of nesting for the American crocodile beginning in 1978 when hatchlings were first captured (Gaby, McMahon, Mazzotti, Gillies, & Wilcox, 1985).

2.3 | Data collection

We recorded crocodile capture histories and included events from 1978 to 1981 (Gaby et al., 1985), 1983 to 1993 (Brandt et al., 1995), 1993 to 2009 (conducted by Florida Power & Light Co.) and 1996 to 2005 (Cherkiss, Romañach, & Mazzotti, 2011), largely targeting the hatching season from June to September. The first non-hatchling crocodile was captured in 1983 (Brandt et al., 1995). Systematic monitoring surveys were conducted in the cooling canal system quarterly by UF from 2009 to 2014 (Figure S5a). Crocodiles were captured at night from a boat using a self-locking snare, tongs, or, if smaller than 1 m, by hand. We used a tape measure to obtain measurements of total length (TL: from tip of snout to tip of tail dorsally) to the nearest centimetre, and measured mass using a spring scale to the nearest gram as described by Mazzotti and Cherkiss (2003). Sex was determined in crocodiles greater than 1 m (TL) when possible. Crocodiles were assigned to size class based on total length: hatchlings (TL < 65 cm), juveniles (65 ≤ TL < 150 cm), subadults (150 ≤ TL < 225 cm) and adults (TL ≥ 225 cm). Individuals with damaged or missing tails were removed from analysis. Each individual crocodile was permanently marked by notching the dorsal edge of a unique series of caudal scutes (Mazzotti & Cherkiss, 2003). In 2004, passive integrated transponder (PIT) tags were implanted subcutaneously along the left side of the tail adjacent to the vent. Each crocodile was then released at capture site following data collection.

2.4 | Estimation of age- and time-specific survival

We estimated age-specific survival rates from capture-recapture histories of marked and known-aged crocodiles only (i.e., individuals first captured as hatchlings). Because all marked crocodiles are not recaptured every subsequent year, we performed capture-recapture (CR) analyses (Lebreton, Burnham, Clobert, & Anderson 1992) to estimate annual survival rates defined as proportion of crocodiles that survived between time t and $t + 1$ (later referred to as ϕ_t) and recapture rate at time t (p_t) in the same statistical model. More than 90% of hatchlings were caught between June and August (Figure S5b), thus we defined June 1st as the starting point for each year (noted t) in CR analysis, consistent with south Florida nesting reports (Kushlan & Mazzotti, 1989; Ogden, 1978). Annual survival rate ϕ_t is, therefore, defined as proportion of surviving crocodiles from June 1st at year t to May 31st at year $t + 1$. We estimated apparent survival of crocodiles because the TP study site is not demographically closed and permanent emigration could not be distinguished from death.

First, we modelled recapture rates and fitted models with constant, time- and age-dependent recaptures. Because capture rate effort varied over time, we also considered a categorical time variable with four modalities that corresponds to the different monitoring phases described above (1978–1983; 1984–1994; 1995–2007; 2008–2014) and allowed recapture rate to vary linearly within each time period. Second, we fitted a full age-dependent model for survival because we had no a priori knowledge about the age structure of crocodile survivorship. From the observed pattern of 25 age-specific survival rates

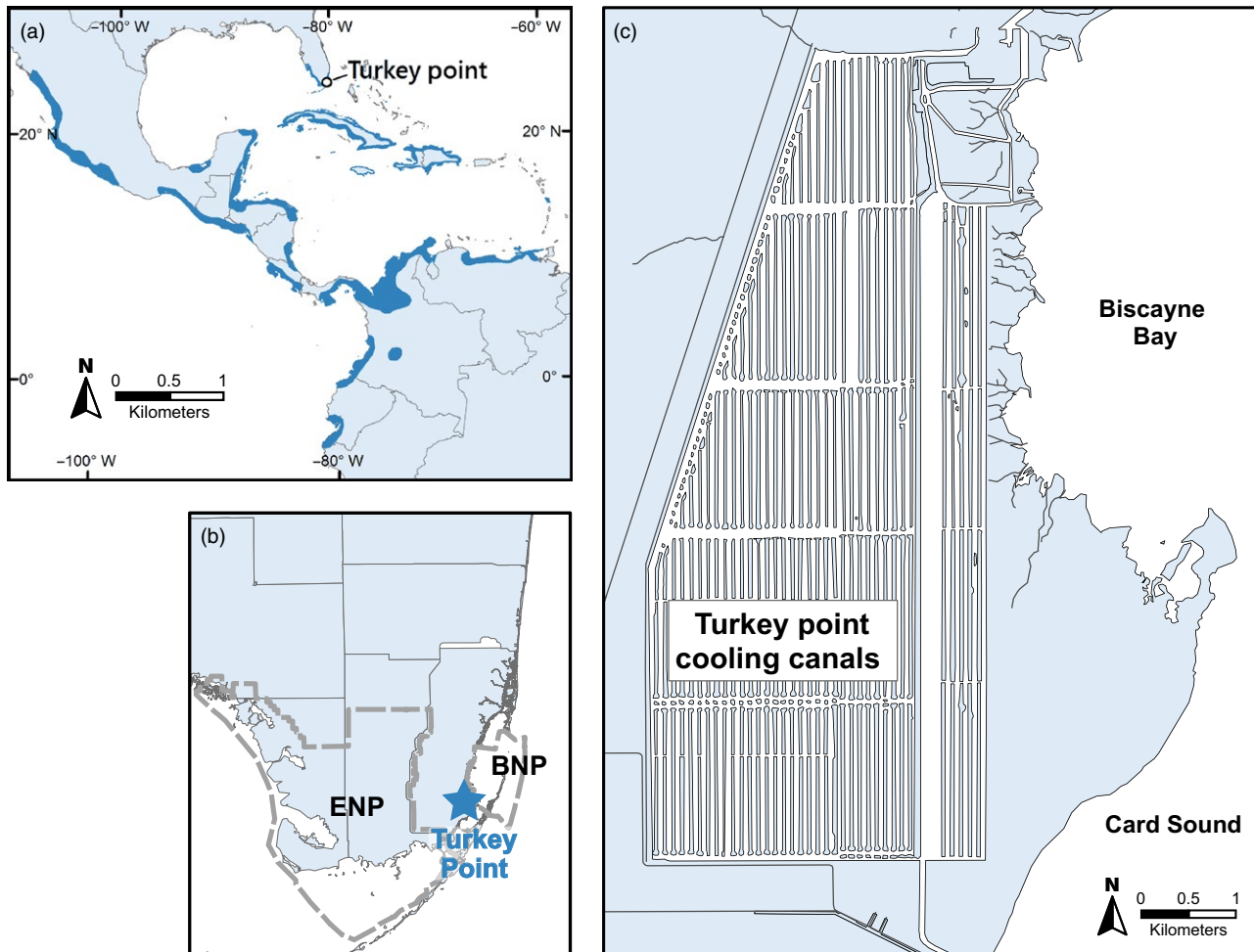


FIGURE 1 (a) Map of distribution range of the American crocodile (*Crocodylus acutus*) highlighting its northernmost region in south Florida. (b) Turkey Point power plant (denoted by a star) is located adjacent to Biscayne Bay within Biscayne National Park (BNP), and northeast of Everglades National Park (ENP). (c) Map of the cooling canal system of Turkey Point which is the study site for a long-term, individual-based monitoring programme of American crocodiles [Colour figure can be viewed at wileyonlinelibrary.com]

(oldest crocodile ever captured at TP was 25 years of age), we pooled age classes showing similar survival rates to decrease the number of degrees of freedom and to increase precision of survival rate estimates.

For all steps, we performed our model selection with Akaike information criterion corrected for sample size (AIC_c) and selected the model with smallest AIC_c as the most parsimonious that best described our data (Burnham & Anderson, 2002). We fit all CR models to crocodile capture history data using MARK software (White & Burnham, 1999) in R (R Core Team 2015) through RMARK package (Laake, 2013).

2.5 | Inferring age-specific fecundity from body length

In south Florida, female crocodiles reach sexual maturity when they attain a total body length of 225 cm (Mazzotti, 1983) and produce an average clutch size of 38 eggs (Kushlan & Mazzotti, 1989). We estimated population-level age-specific reproduction indirectly by (1) modelling body growth of female crocodiles from known-aged individuals ($N = 45$ females sexed with confidence) and (2) calculating

age-specific proportion of females larger than the previously established body size threshold of 225 cm (Mazzotti, 1983). We modelled total length as a function of age using generalized linear models. More than 80% of individuals had one or two measurements only, and a single individual had 10 or more measurements; following Bolker et al. (2009), who advise for the addition of random effects when there are 10–20 samples per individual, we did not include a random intercept on individuals. Using all crocodiles of known age, we compared a constant model, with three models including linear, quadratic, and cubic terms of age incrementally (i.e., first-, second- and third-order polynomials) on a (natural) log–log scale. Predictions of the best model were used to estimate the age-specific proportion of reproductive females based on the predicted percentile of females from 0 to 25 years that were larger than 225 cm (reading 5.41 on a log scale).

2.6 | Population growth rate

We obtained an estimate of population growth rate (λ) of the TP crocodile population from an age-structured Leslie–Lefkovich matrix

demographic model (Lefkovich, 1965; Leslie, 1945). The constructed pre-breeding matrix (noted L) is of dimension 25, maximum age of crocodiles observed at TP (Table S2). We parameterized the matrix entries from estimated age-specific survival rates (ϕ_i) for sub-diagonal parameters (P_i) and from the product of sex ratio (estimated to be 0.59 in favour of females, Kushlan & Mazzotti, 1989), age-specific proportion of reproductive females, average clutch size (CS_i) estimated to be 38 eggs per female, (Kushlan & Mazzotti, 1989) and age-specific survival rates for age-specific fecundity parameters (noted F_i). F_i entries hence equal $CS_i \times SR_i \times \phi_i$.

The resulting age-class population matrix L takes the form:

$$\begin{bmatrix} F_1 & F_2 & \dots & F_{24} & F_{25} \\ \phi_1 & 0 & \dots & 0 & 0 \\ 0 & \phi_1 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \phi_{24} & 0 \end{bmatrix}$$

We computed asymptotic population growth rate λ as dominant eigenvalue of L (Caswell, 2001; Leslie, 1945). In addition to population growth rate, we derived stable age distribution (Table S2) returned by the right eigen vector of the projection matrix (Caswell, 2001), and generation time \bar{T} (Leslie, 1966) as average age of females at time of egg laying.

Finally, we quantified relative influence of changes in fecundity or survival on population growth rate by running a sensitivity analysis (Caswell, 2000) with two main goals. First, we wanted to assess consequences of poor estimations of some demographic rates on computed population growth rate. In the TP crocodile population, fecundity parameters are uncertain as we estimated proportion of reproductive females indirectly from age-specific body length and age-independent estimates of sex ratio and clutch size. Second, sensitivity analysis emphasizes key demographic rates that should be targeted in management plans (see Crouse et al., 1987). In order to make comparisons among demographic rates easier, we calculated and presented elasticities (e_{ij}), which are proportional sensitivities, as follows:

$$e_{ij} = \frac{a_{ij}}{\lambda} \cdot \frac{\delta\lambda}{\delta a_{ij}} \quad (1)$$

3 | RESULTS

3.1 | Annual recapture and survival rates

A total of 7,427 crocodiles were captured as hatchlings within the TP system. A total of 594 crocodiles were recaptured at least once (2.75 ± 1.36 recaptures per individual) and used for subsequent body growth analyses; of these, 380 were recaptured beyond the hatchling stage (Table S3). Time between recaptures ranged from within the same day to almost 24 years (8,734 days), with 68% of recaptures occurring within 1 year.

The best CR model for recapture rate included the effect of time period and its linear variation (Table 1). Recapture rate of crocodiles was virtually null (<0.001) from 1979 to 1983, then reached highest

rates in 1984 (0.42 ± 0.20) and 1986 (0.43 ± 0.15) before decreasing to 0.03 ± 0.02 in 1995; followed by a period of low recapture rate (0.03 ± 0.01 – 0.12 ± 0.03) from 1995 to 2007. From 2008 to 2014, when monitoring surveys were conducted, recapture rates ranged between 0.08 ± 0.02 and 0.36 ± 0.04 , but decreased with each subsequent year of survey (Figure S6).

Apparent survival of crocodiles was strongly age structured, a pattern which was best described by five age classes (hatchling survival between 0 and 1 years; yearling survival from 1 to 2; survival between 2 and 3 years of age; survival between 3 and 12 years of age; and survival of individuals aged >12 years, time period and its within-period linear variation (Table 1). Compared with other age classes, annual survival of hatchlings was lowest (0.16 ± 0.01). Annual survival of 1-year old crocodiles averaged 0.59 ± 0.06 . Survival then increased steadily from 0.80 ± 0.08 and 0.82 ± 0.02 for age classes 2–3 and 3–12, respectively, to reach 0.88 ± 0.03 after 12 years of age (Figure 2).

3.2 | Body growth

The body growth model including both linear and quadratic terms of age received greater statistical support than the constant model ($\Delta AIC = 3160.21$) and the model with the linear term only ($\Delta AIC = 1175.56$). Adding third-order polynomial term of age did not improve model fit ($\Delta AIC = 0.73$) (Table 2). Growth rate in total length decreased with age, but did not reach a plateau (Figure 3a). Average body growth rate progressively decreased with age (hatchlings: 0.11 ± 0.03 cm/day (38.52 ± 11.92 cm/year); juveniles: 0.05 ± 0.008 cm/day (18.94 ± 2.80 cm/year); subadults: 0.04 ± 0.01 cm/day (14.31 ± 0.65 cm/year); adults: 0.03 ± 0.01 cm/day (12.18 ± 0.54 cm/year)).

TABLE 1 Model selection for recapture probabilities (p) and survival probabilities (ϕ) of American crocodiles (*Crocodylus acutus*) in the Turkey Point system, Florida. K is the number of parameters in the model; deviance is the deviance of each model; ΔAIC_c is the difference of each model relative to the best model, according to their Akaike information criterion corrected for small sample size; ω_i is the weight of evidence that each model is the best; a = age (continuous); a_{cl} = age classes; t = time (continuous); t_{cl} = time classes * model selected

Model description	K	Deviance	ΔAIC_c	ω_i
Recapture probabilities (p)				
$\phi(a_{cl}), p(.)$	6	1294.25	227.69	0.00
$\phi(a_{cl}), p(t)$	36	1015.78	9.56	0.01
$\phi(a_{cl}), p(t_{cl})$	8	1124.16	61.56	0.00
$\phi(a_{cl}), p(t_{cl} \times t)$	11	1056.53	0	0.99*
Survival probabilities (ϕ)				
$\phi(.)$, $p(t_{cl} \times t)$	7	1427.32	362.77	0.00
$\phi(t)$, $p(t_{cl} \times t)$	26	1283.57	257.19	0.00
$\phi(a)$, $p(t_{cl} \times t)$	20	1046.13	7.67	0.02
$\phi(a_{cl}), p(t_{cl} \times t)$	11	1056.53	0	0.98*

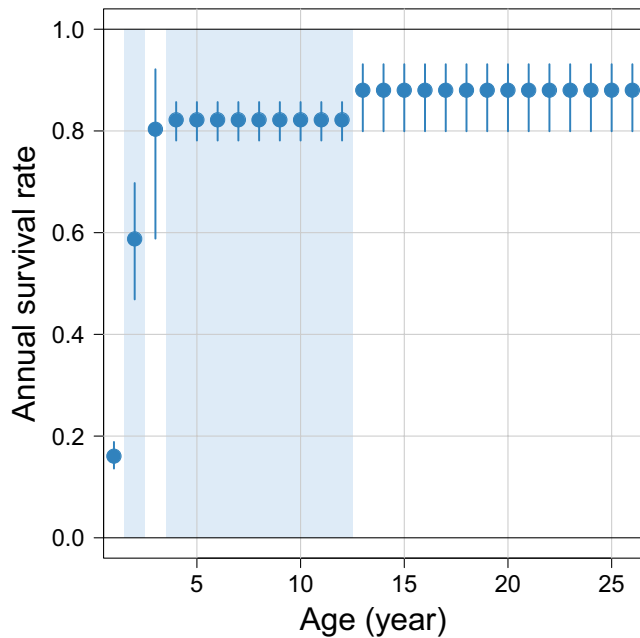


FIGURE 2 Results of the capture–mark–recapture analyses of American crocodiles (*Crocodylus acutus*, $N = 7,427$) monitored individually from 1978 to 2014 at Turkey Point, Florida, USA. Estimation of the average age-specific survival rates and 95% confidence intervals, shaded areas indicate the different age classes during which survival was homogeneous among individuals (five age classes were retained) [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Fecundity

Estimated clutch size for *C. acutus* in Florida is 38.00 ± 9.45 eggs per female at population level (Kushlan & Mazzotti, 1989; but see Charruau, Thorbjarnarson, & Hénaut, 2010; Thorbjarnarson, 1988 for regional clutch size differences). From the predicted body length of 225 cm for reproductive females (Mazzotti, 1983), >5% of females were estimated to be reproductive at 8 years of age among TP crocodiles (Figure 3b, Table S1). Age-specific percentage of reproducing females then steadily increased until 18 years of age, after which virtually all females were said to be reproducing (Figure 3b, Table S1). Age-specific fecundity ranged from 0.45 for 7-year-old females to 22.2 for females aged 20 and older (Table S1).

TABLE 2 Model selection for growth analysis of American crocodiles (*Crocodylus acutus*) in the Turkey Point system, Florida. K is the number of parameters in the model; AIC is the Akaike information criterion; ΔAIC is the difference of each model relative to the best model; ω_i is the weight of evidence that the i -th model is the best; * model selected

Model	K	AIC	ΔAIC	ω_i
Constant	2	2008.58	3160.21	0.00
First-order polynomial	3	23.93	1175.56	0.00
Second-order polynomials	4	-1151.63	0	0.59*
Third-order polynomials	5	-1150.90	0.73	0.41

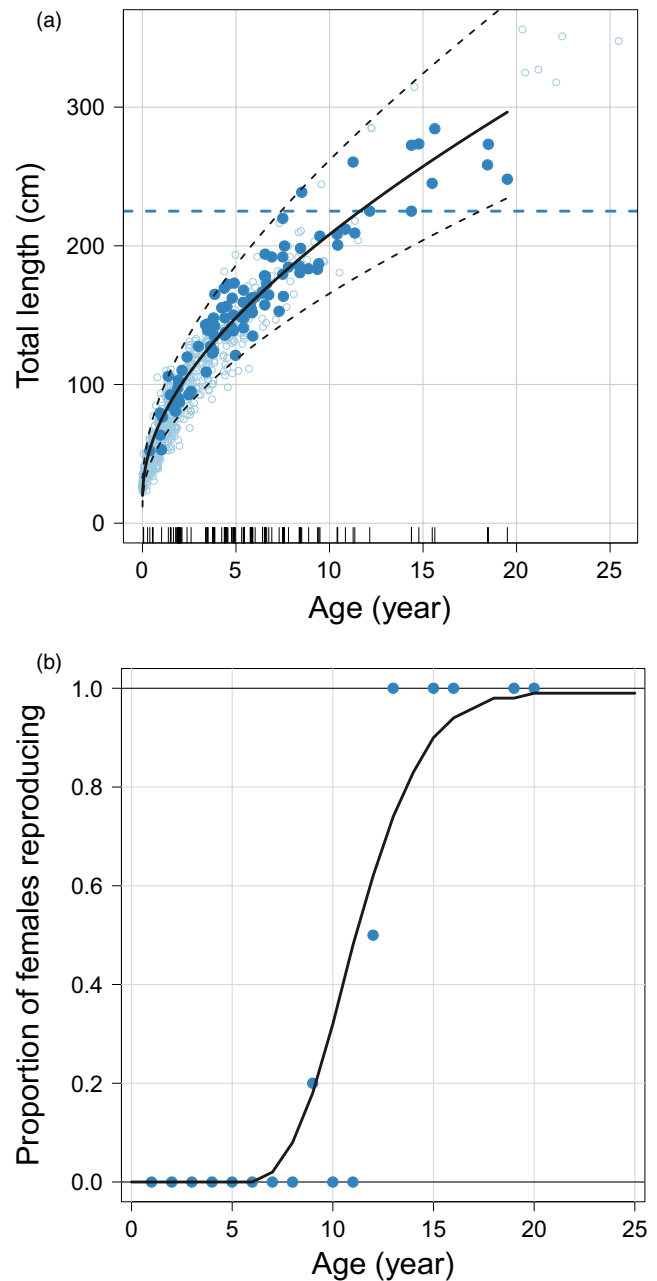


FIGURE 3 (a) Total body length (TL) as a function of age for American crocodiles (*Crocodylus acutus*) (open circles = males, solid circles, bold line = females; horizontal dashed line at TL = 225 cm); (b) estimation of proportion of age-specific reproductive female crocodiles at Turkey Point (solid circles = observed; bold line = predicted) [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Annual population growth rate

We estimated the asymptotic population growth to $\lambda = 1.04$, which corresponds to a population growth rate of $r = \ln(1.04) = 0.04$ ($r = \ln[\lambda]$, see Caswell, 2001, p. 92), suggesting that the TP crocodile population has been growing since 1978 by 4% each year on average. Corresponding generation time was $\bar{T} = 16.2$ years. The stable age distribution indicates that hatchlings should asymptotically represent

64% of the crocodile population with rapidly decreasing proportion of older age classes (Table S2).

3.5 | Sensitivity analysis

Elasticity analysis shows that population growth rate is highly sensitive to survival of crocodiles during the juvenile period of their life cycle ($e > 6\%$ until 8 years old). Sensitivity of population growth rate to variation in survival of crocodiles then steadily decreases for individuals aged >8 years, until it becomes negligible after 19 years of age as expected for any age-structured population ($e < 1\%$; Figure 4). Grouped by age classes, total sensitivity is 0.063 for hatchlings, 0.378 for juveniles (until 7 years of age) and 0.496 for adults (from 8 years old). Overall, the relative sensitivity of population growth rate to changes in fecundity parameters (Figure 4) was much lower than its relative sensitivity to survival rates (sum of elasticity was 0.063 and 0.934 for fecundity and survival parameters, respectively). Elasticity to sex ratio was 0.063, and $\lambda = 1.030$ under the assumption of an even sex ratio.

4 | DISCUSSION

4.1 | Life histories of long-lived reptiles

Long-lived species such as seabirds and large mammals share the biological property of population growth rates being impacted more by changes in adult survival than by any other demographic parameter

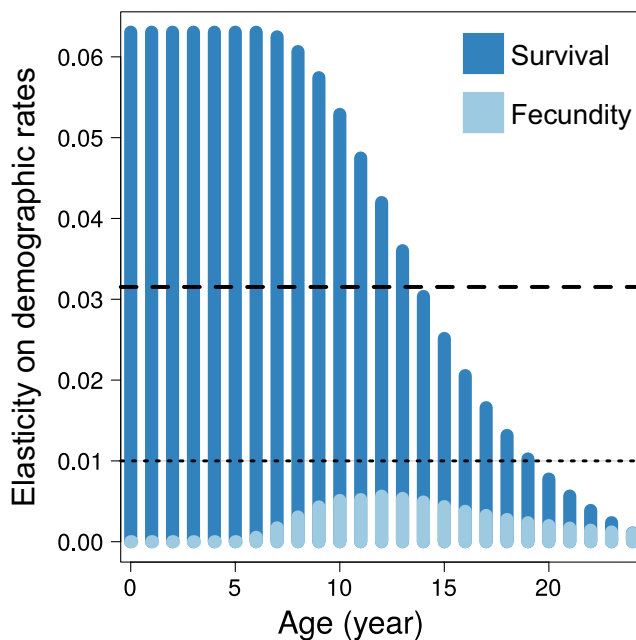


FIGURE 4 Relative contribution of fecundity and survival parameters as provided by elasticities of population growth rate to changes in the projection matrix elements for the American crocodile (*Crocodylus acutus*). A horizontal dashed line indicates half of the maximum value; a dotted line indicates a contribution of 1% [Colour figure can be viewed at wileyonlinelibrary.com]

(Gaillard & Yoccoz, 2003; Sæther & Bakke, 2000). Because of a relatively long life expectancy and a known minimum of 25 years, we also predicted both high adult survival rate and high elasticity to adult survival rate for *C. acutus* and we indeed observed a high adult survival in the TP American crocodile population. More unexpected for a long-lived species was the relatively high sensitivity of population growth rate to survival rate of crocodiles *before* they reached adulthood, which was of similar magnitude than for adult survival rate (elasticities: $\sim 38\%$ for juveniles vs. $\sim 50\%$ for adults). We expected low elasticity on fecundity rates, and we found that, indeed, small variation in crocodile fecundity would affect population growth rate only marginally.

A literature review of 16 large, long-lived reptile species for which 30 demographic datasets were available (Salguero-Gómez et al., 2016) places the American crocodile in context with other long-lived reptiles. The relative sensitivity of λ to juvenile survival was 29% on average compared with 60% for adult survival among these large, long-lived reptiles. The American crocodile mirrors a pattern shared by several species of long-lived reptiles (Figure 5). Several other crocodylian and chelonian species, such as freshwater crocodile (*Crocodylus johnstoni*) or green sea turtle (*Chelonia mydas*), had high sensitivity to juvenile survival that exceeded 40% (Figure 5). The importance of the sub-adult stage for demography of long-lived reptiles is, however, more marked for increasing populations ($\lambda > 1.0$), where sensitivity of population growth to juvenile survival was 34% and 51% to adult survival. The previously reported pattern of greater elasticity of population growth to adult survival than to juvenile survival was more evident for declining populations ($\lambda < 1.0$) where elasticity to adult survival was 68% and almost three-fold greater than juvenile survival at 24% (Gaillard et al., 2000). Loggerhead turtles (*Caretta caretta*) showed an even more divergent pattern with a sensitivity to juvenile survival reaching almost 60%, with a decreasing population ($\lambda = 0.95$, Figure 5).

Here, in this population of *C. acutus*, expected impacts of demographic rates such as fecundity and adult survival rates on population growth rate differ from other long-lived vertebrates and were strongly correlated with life-history traits. Within reptiles, a generation time of >15 years places American crocodiles as long-lived close to the slow end of the slow-fast continuum of life-history traits (Gaillard et al., 2005). Crocodiles, however, display characteristics shared by both a fast (average clutch size: 38 eggs; fecundity over 20 after 15 years of age) and a slow species (high adult survival rate, long life span). Similarly, loggerhead turtles, with a slow maturation and high fecundity, show similar patterns of relative sensitivity as the American crocodile (Crouse et al., 1987), suggesting that long-lived reptiles respond to evolutionary pressures, such as predation, competition and environmental effects, differently than birds and mammals. However, the mechanisms that lead to such a contrast in life-history strategies remain to be determined. As poikilotherms with comparatively low maternal care, long-lived reptiles cannot reach body growth rates as high as those of birds and mammals. Slow body growth, in turn, acts as a constraint on life histories of large reptiles, and the consequence is delayed maturity and first reproduction. In this unusual life-history strategy among long-lived species, high reproductive output of female

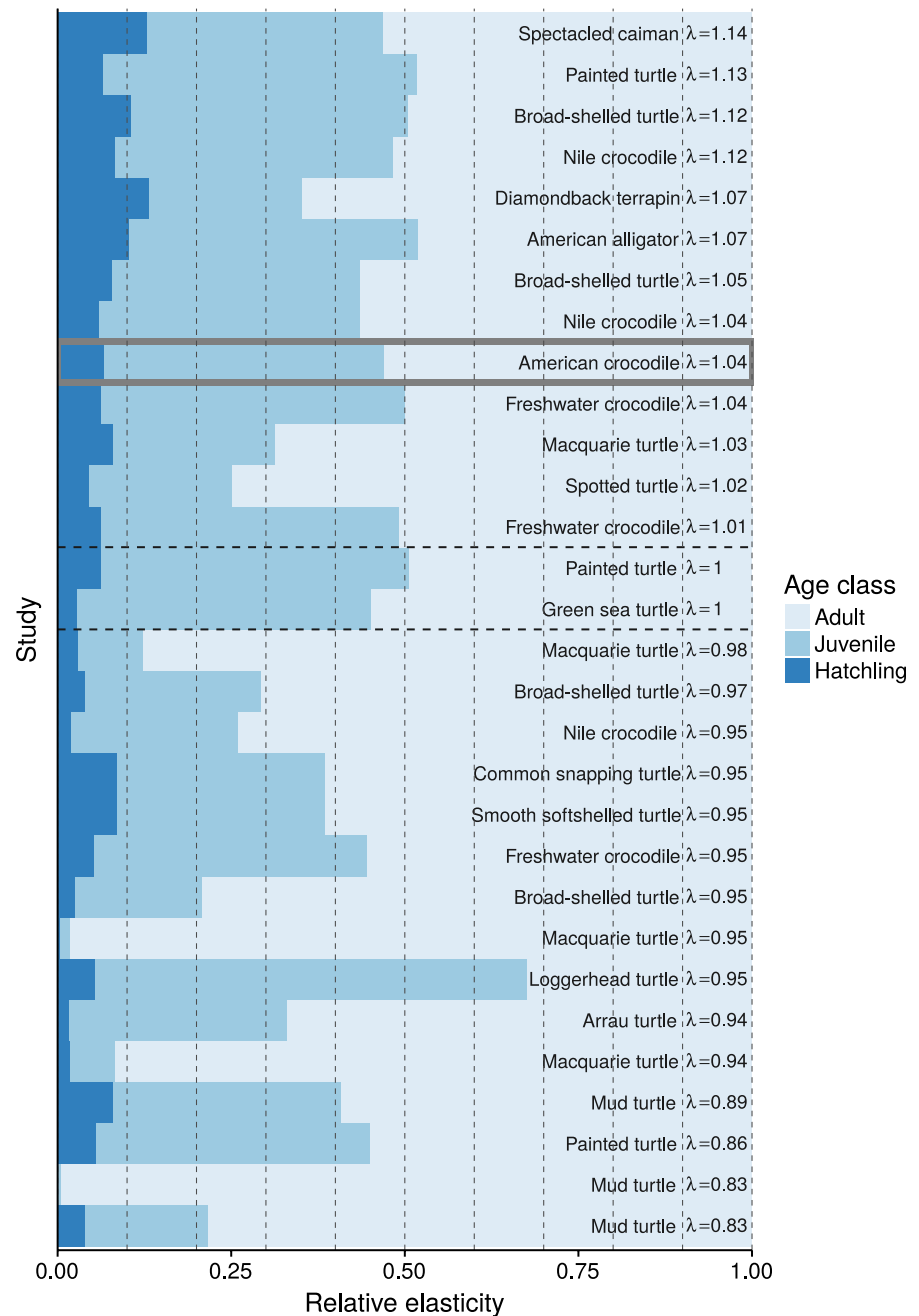


FIGURE 5 Interspecific comparison of elasticity of population growth rates to survival rates of hatchlings, juveniles (between age 1 and the age at first reproduction) and adults in long-lived reptiles taken from datasets presented by Salguero-Gómez et al., 2016 (see Table S4 for list of data sources used in this review). Data for American crocodiles (*Crocodylus acutus*) are provided for comparison using our analyses [Colour figure can be viewed at wileyonlinelibrary.com]

American crocodiles likely compensates for their relatively late age at first reproduction. However, we estimated that juvenile crocodiles rapidly reached an annual survival rate >0.8 within 3 years of life in this study population, close to observed adult survival rate, and in agreement with high sensitivity of population growth rate to survival of this life stage.

Slow species generally combine high longevity and low reproductive output (Gaillard et al., 1989). As a result, adult survival rate has greater elasticity than juvenile survival rates as is expressed in 19 of 23 long-lived mammal species in Heppell et al. (2000)'s review. However, some species can achieve similarly long generation time with contrasting life histories, but there is variability both within families and even within genera. In 3 of the 23 long-lived mammals in the same review

(Heppell et al., 2000), juvenile survival had higher elasticity than adult survival (i.e., chimpanzee [*Pan troglodytes*], elephant [*Loxodonta africana*], killer whale [*Orcinus orca*]), seemingly in relation to the combination of a late age at first reproduction and a long generation time. In a review of 49 species of birds, which included a wide range of orders from Passeriformes (passerines) to Cicconiformes (storks), Sæther and Bakke (2000) highlighted that long-lived species (waders, owls, terns) displayed higher adult survival elasticities with an early age at first reproduction, however with a large clutch size. Furthermore, long-lived reptiles have both a large clutch size and later age at first reproduction which leads to higher elasticity of juvenile survival (Figure 5). These particular characteristics call for a less restrictive association of life histories along the slow-fast continuum, to account for large reptiles

(i.e., sea turtles, crocodylians) or other long-lived bird species, and for a better consideration of their particular demography, which should be accounted for in conservation and management policies. As a side note, it is interesting that the relationship between λ and juvenile survival elasticity apparent in long-lived reptiles also holds true in long-lived mammals (Heppell et al., 2000).

4.2 | Age structure of American crocodile demographic rates

Most previous demographic studies on American crocodiles used size classes to capture individual heterogeneity in demographic rates (e.g., Richards, 2003) likely because age was not exactly known. Focusing on known-aged crocodiles, we found that age is a major structuring factor of American crocodile demographic rates as generally reported for long-lived species. In our population, age accounts for 26% of observed variation in survival. Moreover, because age accounts for 85% of body size (i.e., total length), our results supports the use of body size in practice when age of crocodiles is unknown (Webb, Manolis, & Buckworth, 1983; Webb et al., 1978; Woodward et al., 1995). This is one of the few studies to use accurately aged crocodiles and is one of the first to extend beyond 10 years of demography (Moler 1991) and provides minimum longevity of 25 years for *C. acutus*; additional simulation models estimate longevity at 49 years (Richards, 2003) and a range of 40–56 years for crocodylians in captivity (Levy, 1991). Large and thus older crocodiles are captured with less frequency both because of wariness and inaccessibility; thus, estimates are limited to crocodile captures made during this time period, and we acknowledge that there certainly must exist crocodiles older than 25 years old in south Florida and elsewhere throughout its range.

Crocodile survival in the Turkey Point system was clearly age dependent and survival estimates increased with age (Figure 2). Here, a hatchling crocodile survival rate of 0.16 from 35+ years of monitoring at TP was within previous estimates in south Florida (0.07–0.43 at Key Largo, FL, Moler, 1991; and used in simulations in Richards, 2003); but was higher than 0.10 in Florida Bay (Mclvor, Ley, & Bjork, 1994) or 0.09 after 9 years at TP (Brandt et al., 1995), and elsewhere in its range (0.05 in Panama, Balaguera-Reina, Venegas-Anaya, Sanjur, Lessios, & Densmore, 2015). This TP hatchling estimate is also higher than in other crocodylians (i.e., gharials [*Gavialis gangeticus*]: 0.06 Hussain, 1999; 0.05 *C. niloticus*, Blake & Loveridge, 1975; 0.08 *C. johnstoni*: Webb et al., 1983). In comparison with other reptiles, survival rate of young *C. acutus* fell within the range for some other reptiles: snakes (0–0.27 Bonnet, Naulleau, & Shine, 1999) and chelonians (0.01–0.67 Heppell, 1998). The difference in juvenile survival we see may be due to a multitude of factors, including environmental and habitat differences, interspecific and intraspecific competition, and other stochastic pressures, as well as methodological differences where imperfect detection of marked animals, if not accounted for, leads to underestimation of survival. Other biological factors may account for the relatively high survival of juvenile American crocodiles, in addition to the prey availability and physical structure of the TP system that may have

traditionally been good crocodile habitat. Cannibalism has been documented for hatchling mortality at TP (Richards & Wasilewski, 2003). For instance, 40 PIT tags that belonged to hatchlings, and in some cases juveniles, have been detected in the stomachs of 25 individuals (F. Mazzotti, unpubl. data). Similarly, predation and vulnerability to both flooding and desiccation are also factors that affect hatchling survival (Mazzotti, 1983). By the time crocodiles reach 4 years of age, our model shows survival rates that exceeded 80% which may reflect a release from the pressures of cannibalism and predation, and did not show a decrease in older crocodiles.

In several large poikilotherms, such as crocodylians, age at first reproduction has been determined by size and not age per se (Magnusson, 1983), but additional factors such as early reproduction or slow growth rate challenge this idea (Charruau et al., 2010). We used the accepted minimum size at maturity of *C. acutus* in south Florida to be 225 cm (Mazzotti, 1983), and using this threshold body size, we found that age at first reproduction was attained at a minimum of 7 years of age in our study, but only 2% of all females were estimated to be reproducing at this age. Other estimates of first reproduction in *C. acutus*, including in south Florida, were at 10 years of age (Richards, 2003), at 9 years of age (Moler 1991) and at 10 years of age in Haiti and Jamaica (Thorbjarnarson, 2010). At 13 years of age, an estimated 62% of female crocodiles were reproducing in this study, similar to local reports (LeBuff, 1957; Ogden, 1978), and similar to what is reported for other crocodylians (*C. niloticus*, Graham, 1968; multiple crocodylians, Yangprapakorn, Cronin, & McNeely, 1971). By age 18, more than 95% of females (Table S1) of *C. acutus* were presumed to be reproducing in the TP system. This breeding effort is higher than recorded in Everglades National Park, Florida (72% Mazzotti, 1983), and in Haiti (63.8% Thorbjarnarson, 1988) for this species, but is within the range for other crocodylians (*C. niloticus* 80% in Zambia, Cott, 1961; 67% in Botswana, Blomberg, 1982; 88% in Kenya, Graham, 1968); 90% *C. johnstoni* in Australia (Webb et al., 1983), and 68% *Alligator mississippiensis* in Louisiana (Chabreck, 1966).

5 | CONCLUSION

The American crocodile has adapted to the man-made conditions at Turkey Point (Cherkiss et al., 2011; Mazzotti, 1983; Mazzotti et al., 2007) and has experienced an estimated average growth rate of 4% annually, based on our models, since the first hatchlings were discovered in 1978 (Brandt et al., 1995; Gaby et al., 1985). Continued protection of the American crocodile and its nesting and coastal habitats are important, particularly in south Florida where monitoring and management efforts have had a positive impact on the conservation status of this threatened species (Mazzotti et al., 2007). Presently, the ability to capture large crocodiles in higher numbers will provide us with improved survival estimates, while continued monitoring of hatchlings into adulthood is important to determine accurate demographic information. Juvenile and subadult crocodiles are, indeed, critical stages to increase population growth. Protection, management and monitoring should thus extend to include these age

classes. This study emphasizes the need for long-term monitoring programmes to provide accurate demographic data which are important for species survival and in cases of threatened species, towards species recovery. As the world's largest ecosystem restoration project occurs in south Florida to protect the Greater Everglades, indicators of change, such as the American crocodile, can further be used to quantify ecosystem responses to restoration and provide a guide for how management efforts can benefit both species and natural lands (Mazzotti et al., 2007). In light of our findings, crocodiles may reflect a more general life history, with population dynamics common to all long-lived reptiles which calls for continued monitoring and conservation action that extends beyond hatchlings to include younger, pre-reproductive stages (see also Mauger et al., 2012) for successful species conservation.

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AUTHORS' CONTRIBUTIONS

F.J.M., V.B.G., M.C. and J.B. conceived the project and designed field methodology; F.J.M., M.C., J.B. and V.B.G. collected the data; V.B.G. conceptualized and led the writing of the manuscript; C.B., M.B. and V.B.G. developed ideas and designed quantitative methodology; M.B., C.B. and V.B.G. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available at Dryad Digital Repository <https://doi.org/10.5061/dryad.ck5vv> (Briggs-Gonzalez et al., 2017).

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