Consequences of individual removal on persistence of a protected population of long-lived turtles

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Abstract

Box turtles *Terrapene carolina* are long-lived vertebrates found in many habitats throughout eastern North America. Because they routinely live >30–70 years, individuals and populations likely face periodic catastrophic effects from habitat alteration, such as hurricanes and other violent storms, flooding, and climatic perturbations such as cold or drought. We used a dataset based on a 16-year mark-recapture study of a Florida box turtle population inhabiting an isolated island to model the effects of rare and chronic removal of individuals from the population. 'Removing' individuals based on actual sampling records allowed us to compare the resulting effects on population structure and persistence with the known demographic characteristics of the population. For the increasing population, removal had no effect on population size over a projected 50-year time span. However, only the increasing population could sustain an annual loss of up to 56 individuals (3.8% of our initial model population) per year. Beyond this level of annual removal, the population would eventually go extinct. Both the stable and declining populations were projected to become extinct by year 50, regardless of removal intensity. Irrespective of frequency, a pre-reproductive season loss leads to a smaller population than a post-reproductive season loss. These results have implications for understanding the effect of individual removal on population persistence of declining box turtle populations.

Introduction

Biological communities are composed of organisms with a continuum of temporal life-history traits, from those whose life spans are short with rapid population turnover, to species adapted to relative habitat stability with very long life spans (Pianka, 1970). Whereas many studies have examined species with short life spans and their response to fluctuating environmental conditions, the logistics and analytical difficulties (e.g. McMahon *et al.*, 2009) of following the responses of long-lived species to environmental changes have limited understanding of the ways such species react and adapt. Although long-term studies on long-lived species are relatively few because of extended generation times, models using empirically derived demographic rates help researchers understand how long-lived species evolved to handle stressful conditions.

Environmental change can occur slowly or rapidly, whether it be gradual climate change through thousands of years (although still short-term in geological time) or from stochastic disturbance events, such as flooding, hurricanes or other violent storms, or severe fires. Disturbances are well-known for their importance in structuring communities (Turner *et al.*, 2003), a disturbance being defined as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes in resource pools, substrate availability, or physical environment' (White & Pickett, 1985). It seems reasonable to hypothesize that the longer a long-lived species lives, the more likely it will be exposed to some form of disturbance that could affect population stability and persistence. At the same time, a long life span actually may buffer against extreme environmental disturbances since reproductive output is extended over a longer period of time when habitat conditions could possibly improve (Morris *et al.*, 2008; Lescroël *et al.*, 2009).

A number of co-evolved life-history traits are associated with long lives, including extended parental care (whether through pre-hatching yolk investment or post-hatching/birth care), delayed reproduction, reduced annual fecundity, low recruitment and high adult survivorship (Congdon, Dunham & Van Loben Sels, 1993; Heppell, Crowder & Menzel, 1999; Musick, 1999). These traits allow for individual replacement over a long-time span, rather than saturating the environment with large numbers of offspring produced annually. With the exception of post-hatching parental care, most chelonians tend to exhibit such 'typical' life-history

characteristics, and many turtles are exceptionally long-lived (Gibbons, 1987; Litzgus, 2006; Ernst & Lovich, 2009). Even when turtle life-history appears contradictory to other long-lived species, such as when clutch sizes (CS) are large, the outcome is often the same (i.e. low recruitment). For example, whereas some turtles can produce many eggs in one season (snapping turtles, many softshells, sea turtles), nest and offspring survival is thought to be quite low and many of these species do not nest annually. As such, few hatchlings become adults, and high fecundity at one or even several points in time does not result in substantial recruitment. In turtles that produce few eggs annually, hatchling survival may actually be much higher than previously thought (Pike et al., 2008). Thus, increased juvenile survivorship compensates for a small number of eggs, but the effect is still a relatively low recruitment rate that maintains population size.

Selection for long generation times probably occurs under stable temporal and spatial environmental conditions, since the co-evolved life-history traits of long-lived species make it unlikely that species could adjust to many sequential sudden catastrophic events or rapidly changing environments. For example, turtles do not generally show plasticity in CS or annual frequency to offset increased predation, in contrast to the density-dependent reproductive compensation observed among many birds. A notable exception to the density-dependence scenario is *Chelodina rugosa* that is fast-growing, early maturing and highly fecund relative to other turtles, and thus resilient to increased mortality (Fordham, Georges & Brook, 2007, 2009). Instead, most turtles and other long-lived species might be said to trade-off the benefits of a quick response to fluctuating environments for long-term population stability. This imposes a dilemma, however, in that a long life (say, >30–70 years or more; Graham & Hutchison, 1969; Henry, 2003) could increase the likelihood that populations would be exposed to significant catastrophic events or other stochastic perturbations to which their life-history traits would be ill-suited for short-term recovery (Rowe, 2008).

Given the likelihood of experiencing some form of disturbance, it seems questionable that the responses of long-lived species would be so restrictively canalized as to prevent recovery through time, and that some life-history traits might be more plastic than heretofore recognized (Spencer, Janzen & Thompson, 2006; Spencer & Janzen, 2010; Wolak et al., 2010). Instead, chelonians and other long-lived species have evolved several short-term means of coping with disturbances, such as altering reproductive output in response to changing resources, moving to undisturbed areas, and altering growth rates (Dodd, Ozgul & Oli, 2006; Spencer et al., 2006; Dodd & Dreslik, 2008; Lescroël et al., 2009; Spencer & Janzen, 2010; Currylow, MacGowan & Williams, 2012). Changes in heritable growth rates may be particularly important in a long-lived species' ability to cope with environmental stress (Chapin, Kellar & Pugnaire, 1993).

Chelonian populations are reported to decline substantially when subject to human-caused take or natural events, such as the range expansion of a previously absent predator or a catastrophic storm (e.g. Brooks, Brown & Galbraith, 1991; Garber

& Burger, 1995; Hall, Henry & Bunck, 1999; Balazs & Chaloupka, 2004; Moll & Moll, 2004; Jergenson et al., 2014). In contrast, Dodd and colleagues demonstrated that a series of disturbances (hurricane and tropical storm overwash; habitat alteration during a poorly executed restoration effort) had few long-term effects on the population structure of an island Florida Box Turtle *Terrapene carolina bauri* population. Instead, the turtles tended to move to unaffected areas and to alter their growth rates, presumably in response to a change in resources. Individual and population survivorship, detection probabilities, recruitment, and population growth rates were unaffected by sex or life stage (Dodd et al., 2006; Dodd, Hyslop & Oli, 2012). An already male-skewed sex ratio temporarily became more male-skewed, likely as a result of changes in growth rates affecting the timing of maturity (Dodd & Dreslik, 2008; also see Lovich, Gibbons & Agha, 2014). Some mortality was observed, but the number of dead turtles collected was small. Over a 16-year period, disturbances resulted in little effect on the population.

Nevertheless, some catastrophic events, such as fire (Stubbs, Swingland & Hailey, 1985; Lambert, Campbell & Kabigumila, 1998; Hailey, 2000; Howey & Roosenburg, 2013), clearly have serious effects on terrestrial chelonians. The reason the Egmont Key population of Florida Box Turtles did not decline after potentially severe disturbances may have to do with a lack of significant mortality (84 of 2534 marked turtles; 3.3% over 16-years) in an increasing population. If relatively few turtles succumbed to island flooding and short-term (several years) changes in habitat, then the population simply outlasted the effects of the disturbances. These and the results of a few other studies (e.g. Lovich et al., 2011) suggest that as long as mortality is low and resources are productive, chelonian populations may be relatively unaffected by some disturbances.

What might occur, however, if mortality was significant? To explore this question, we used a dataset based on a 16-year mark-recapture study to model the effects of random removal of individuals from the population. 'Removing' individuals based on actual sampling records allowed us to compare the resulting effects on population structure and persistence with the observed demographic characteristics of the unaffected population. Box turtle populations have declined throughout their range and been subject to large amounts of commercial take for the pet trade (reviewed by Dodd, 2001; Kiester & Willey, 2015); removal of individuals for the pet trade is essentially the same as mortality to the population, and these terms are used interchangeably in this paper. Although few models are available on the effects of individual removal on chelonians other than sea turtles (Congdon, Dunham & Van Loben Sels, 1994; Famelli et al., 2012; Zimmer-Shaffer, Briggler & Millspaugh, 2014), the adverse effects of take on other long-lived invertebrates and vertebrates are well documented (Musick, 1999; Heppell et al., 2005). Whether from simulated 'removal' or from stressors that cause mortality, the results of this study lend further insight into the effects of individual removal by season, sex and life stage on long-lived chelonians and perhaps other species.

Materials and methods

Study area

Egmont Key is a long, narrow, north-south trending island located at the mouth of Tampa Bay, Hillsborough County, on Florida's west-central coast (27°36′04″N, 82°45′40″W). The maximum elevation is 3 m, although most of the island is <1.25 m above mean sea level. The geologic and biotic history of the island is reviewed elsewhere (Franz, Dodd & Bard, 1992; Dodd, Franz & Smith, 1994; Stott & Davis, 2003; Dodd & Griffey, 2005). The island historically has been subject to severe periodic erosion, and nearly half of the island, especially on the west and north-western side, has disappeared since it was mapped by the Coast and Geodetic Survey in 1875 (Stott & Davis, 2003; Dodd et al., 2006).

Two types of habitat disturbances affected the island beginning in the latter half of 1995: hurricanes and extensive exotic vegetation cutting. Four tropical storms passed either directly to the north or west of Egmont Key in the Gulf of Mexico during 1995–1996. In 2004, four additional hurricanes (Ivan, Charley, Frances, Jeanne) passed over or near the island, and overwash extended across the entire southern and central portions of the island (Dodd et al., 2006). Beginning in 1996 and with increasing intensity through the mid-2000s, additional habitat disruption involved attempts to kill large stands of Australian pine *Casuarina equisetifolia* and Brazilian pepper *Schinus terebinthifolius*. Chemical application of herbicide killed large stands of these trees, which were later cut down but not mulched or removed. These efforts resulted in substantial loss of canopy cover and subsequent exposure of leaf litter to intense sunshine, thus elevating temperatures and increasing desiccation. As a result, the habitat structure of large sections of the northern and southern portions of the island were significantly altered (Dodd, 2006) and large amounts of downed woody debris were left in place creating considerable physical obstacles to box turtle movement. The desiccating and temperature effects of canopy removal increased with time and were particularly evident between 2002 and 2006 (C. K. Dodd, unpublished data based on HoBo temperature and humidity data loggers).

Study species

The Florida box turtle is a terrestrial species often found on barrier islands of the southeastern United States (Blaney, 1971; Laerm et al., 2000). Florida box turtles are sedentary omnivores with relatively low fecundity (modal CS = 2, 0–3 clutches per year; Dodd, 1997a), high adult and subadult survivorship (>87%; Dodd et al., 2006, 2012), delayed sexual maturity (in Florida, males reach maturity at 8–9 years and females at 10–11 years; Dodd & Dreslik, 2008), low nest and hatchling survival, and a long life span (potentially >50 years) (Dodd, 2001; Kiester & Willey, 2015). These life-history traits suggest that box turtles might be sensitive to habitat disturbance resulting from hurricanes or other disturbances, especially if these disturbances increase immediate adult mortality or decrease long-term survivorship (Congdon et al., 1994).

Data collection

One to five visits were made per year to Egmont Key 1991–1995, 1997–2002, and in 2006. Surveys (n = 35 sampling periods) lasted from 3 to 5 days. Box turtles were found in all sections of Egmont Key's c. 120 ha and in 9 of the 10 management units designated by the Florida Park Service (Dodd et al., 2006). A total of 2591 individual box turtles were observed 5662 times in this study. More extensive information is presented elsewhere (Dodd et al., 1994, 2006; Dodd, 2001; Dodd & Dreslik, 2008).

Box turtles were sampled by visual encounter searches because these turtles, even as juveniles (Jennings, 2003, 2007), are conspicuous in the thin leaf litter of Egmont Key. Searches initially concentrated on the southern 36.4 ha of the island 1991–1995 but were subsequently extended throughout the island. Captured turtles were identified to sex (males have a concave plastron; females have a flat plastron) or life-history stage [turtles were considered subadult if <120 mm carapace length (CL); Dodd, 1997b], and straight-line CL was measured to the nearest mm. Turtles were given a unique number by notching the carapace, photographed dorsally for future recognition, and released at point of capture.

Demographic parameters

Our study relied on estimates of survival and reproductive parameters reported in previous studies (Dodd, 1997a,b; Dodd et al., 2006, 2012). Dodd et al. (2006) found that annual survival did not differ between reproductive adults and juveniles, or between males and females. We used the same multistate capture-mark-recapture model and one additional year (2006) of data to re-estimate the annual apparent survival probability (S, equal among sexes and age classes), and the probability of becoming reproductive (Ψ, i.e. transition from juvenile/pre-reproductive to reproductive adult stage, conditional on survival) for parameterizing our population model (see below). Likewise, we used the mean CS reported by Dodd (1997b) (2.436 ± 0.132; range = 1–5 eggs) and average sex-ratio (defined here as the proportion of males in the adult population) for the entire study period (SR; 1 F: 2.06 M) reported by Dodd et al. (2012). Dodd (1997b) found that 13.7–41.4% of females were gravid in any 1 year, with a mean gravidity of 25.7% (±SE = 21.8). However, this estimate of breeding probability (BP) yielded a growth rate indicative of a decreasing population, which is inconsistent with the observed increase at Egmont Key (Dodd et al., 2012). With an estimated population of 700 individuals in 1991 and 1480 in 2006 (Dodd et al., 2012), the population increased at a 5% annual rate. Because the average BP was calculated from data collected in 1992–1995 only, we allowed a reasonable 37.7% gravidity to approximate this observed annual growth rate. Also, nesting success was assumed to be 100% as our study population inhabited an island free of mesopredators such as raccoons *Procyon lotor*, opossums *Didelphis virginiana* and domestic dogs.

Estimates of demographic parameters used in this study are summarized in Table 1.

Population model

We built a three-state (pre-reproductive, reproductive female, and reproductive male) deterministic matrix population model (Caswell, 2001), with two 6-month seasonal projection matrices because (1) the box turtle population at Egmont Key has a male-biased sex-ratio, (2) box turtles reach sexual maturity at only 8–11 years-old, so pre-reproductive turtles may remain pre-reproductive for multiple years, and (3) we aimed to evaluate the relative impact of disturbance causing loss of individuals before versus after the reproductive season. During the reproductive season [April–September, represented by matrix **B** (equation 1)], pre-reproductive turtles become reproductive adult males with probability $\Psi*SR$, or reproductive adult females with probability $\Psi*(1 - SR)$, while the remaining $1 - \Psi$ fraction remains pre-reproductive, conditional on survival. Females reproduce with the probability BP and when reproductive, lay a clutch of size CS. Individuals in any stage survive the breeding season with the probability Sm^6 where Sm is the monthly survival, calculated as $S^{1/12}$. The fertility rate of adult females is the sum of fertility of adult females that survived the year, and fertility of pre-reproductive females that survived the year and transitioned to adulthood: $BP*CS*Sm^6 + [\Psi*(1 - SR)*BP*CS*Sm^6] = (1 + \Psi*(1 - SR))*(BP*CS*Sm^6)$. The population projection matrix for the breeding season **B** is then as follows:

$$\mathbf{B} = \begin{bmatrix} (1-\Psi)*Sm^6 & (1+\Psi*(1-SR))*BP*CS*Sm^6 & 0 \\ \Psi*(1-SR)*Sm^6 & Sm^6 & 0 \\ \Psi*SR*Sm^6 & 0 & Sm^6 \end{bmatrix} \quad (1)$$

During the rest of the year (October–March), individuals only need to survive with probability Sm^6. Thus, the population projection matrix for the non-breeding season **N** is as follows:

$$\mathbf{N} = \begin{bmatrix} Sm^6 & 0 & 0 \\ 0 & Sm^6 & 0 \\ 0 & 0 & Sm^6 \end{bmatrix} \quad (2)$$

The asymptotic growth rate was calculated as the dominant eigenvalue of the matrix product **B*N**.

Population Projection and Scenarios

We simulated the box turtle population size for 50 years under various scenarios of loss of individuals, considering intensity, timing, and frequency of loss. When the simulated population went extinct, we recorded time to extinction.

Intensity of loss

Data collected between 1991 and 2006 indicate that as many as 140 individuals (i.e. up to 9.5% of the initial population) could be captured in 1 day, accounting for varying proportions of juveniles, female adults, and male adults, if sampling occurred during the reproductive or the non-

reproductive period. We thus simulated population size after 50 years for a fixed loss ranging from 0 to 140 individuals (in 1 year or every year; see 'frequency of loss' below). Loss was assumed to be proportional to sex and age structure of captured turtles, leading to the seasonal loss vectors $\mathbf{L_B}$ and $\mathbf{L_N}$ (equations 3 and 4).

During the reproductive season, loss was assigned as

$$\mathbf{L_B} = L * \begin{bmatrix} 0.532 \\ 0.290 \\ 0.178 \end{bmatrix}, \quad (3)$$

where L is the total number of turtles lost.

During the non-reproductive season, loss was

$$\mathbf{L_N} = L * \begin{bmatrix} 0.582 \\ 0.280 \\ 0.138 \end{bmatrix} \quad (4)$$

Frequency of loss

Disturbances can be rare, periodic or chronic. Here, we considered the effects of rare and chronic disturbance-related losses: a one-time event that occurs during the first year (choosing another year would not affect the results), and a chronic loss that occurs every year.

Timing of loss

We simulated loss to occur before and after the reproductive season. Immediately prior to the reproductive season, new individuals are about to enter the breeding pool in addition to older individuals that survive the mild winter. After the reproductive season, new individuals have been produced. We predicted a greater population-level impact when loss occurs before than after the reproductive season because the loss of new breeders also represents a loss of potential offspring production. The following equations describe how the initial population is projected under a pre-reproductive versus a post-reproductive loss scenario:

Pre-reproductive loss : $\mathbf{n}(t+1) = \mathbf{B}*(\mathbf{N}*\mathbf{n}(t) - \mathbf{L_N})$ (5)

Post-breeding loss : $\mathbf{n}(t+1) = \mathbf{N}*(\mathbf{B}*\mathbf{n}(t) - \mathbf{L_B})$ (6)

where $\mathbf{n}(t)$ is the population vector at time t. The initial population vector ($\mathbf{n}(0)$) was composed of 100 juveniles, 410 adult females, and 970 adult males, as estimated for the 2006 population (Dodd et al., 2012).

Effects of loss on stable and declining population

The Egmont Key population was increasing at a rate of 5% during 1991–2006. However, this increase was probably allowed by the absence of predators and we must examine the impact of the same scenarios on populations of box turtles that may be stable or decreasing. Our model yields an annual increase of about 5% (see Results). Thus, we also considered the effect of disturbance-related loss in a stable

Table 1 Mean estimates (±SE) of demographic parameters for box turtles at Egmont Key, Florida, 1991–2006

Parameter	Symbol	Mean ± SE
Annual survival[a]	S	0.898 ± 0.006
Recruitment probability	Ψ	0.182 ± 0.015
Breeding probability	BP	0.377 ± 0.050
Clutch size	CS	2.436 ± 0.132
Sex-ratio	SR	0.665 ± 0.017

[a]Annual survival from the study population was 0.898, but the hypothetical decreasing and stable populations were assigned an annual survival of 0.813 and 0.856 respectively (see text).

population, and in a population declining at the rate of 5% per year. To achieve growth rates of 1.000 (stable population) and 0.951 (decreasing population), we lowered the survival from 0.898 (Table 1) to 0.856 and 0.813 respectively.

All analyses were performed using the *popbio* package (Stubben & Milligan, 2007) in R computing environment (R Development Core Team, 2014).

Results

The asymptotic annual population growth rates for the increasing, relatively stable, and decreasing populations were 1.0499, 1.0008, and 0.9505, respectively. Starting with the initial population size of 1480 individuals, the projected population size at year 50 would be 18 973, 1730 and 131 individuals for an increasing, relatively stable and declining population, respectively (Fig. 1).

Under a one-time disturbance event scenario, the increasing population would keep increasing exponentially and reach over 16 000 individuals by year 50, regardless of simulated intensity of loss. At year 50, the stable population would have about the same number individuals as the starting population size (even at the highest simulated loss intensity of 140 individuals a year), but the declining population would have barely 16% of the starting population size.

Under a chronic disturbance scenario, only the increasing population can sustain an annual loss of up to 56 individuals (3.8% of our initial model population, but increasing in succeeding years) per year (Fig. 2a). Beyond this level of annual disturbance-related loss, the population would eventually become extinct, and beyond an annual loss of 60 turtles, all population scenarios (increasing, stable, and decreasing) go extinct within 30 years (Fig. 2). Regardless of the frequency or intensity of loss, a pre-reproductive loss would have a greater population-level impact than the post-reproductive loss (Fig. 2).

Discussion

Although box turtle populations have declined at virtually every location where they have been studied over a long period of time (Dodd, 2001; Kiester & Willey, 2015), the population at Egmont Key increased at a rate of nearly 5% over the 16 years we monitored it. Thus, the Egmont Key population is unusual compared to most terrestrial chelonian
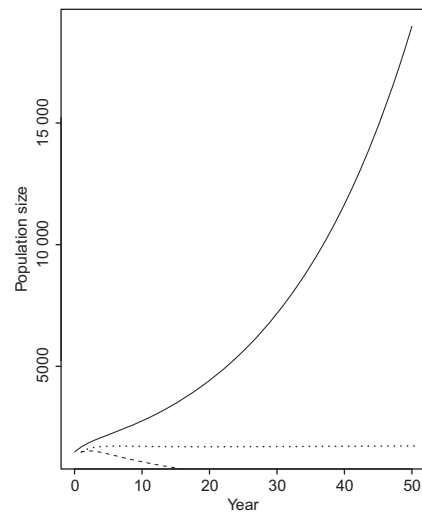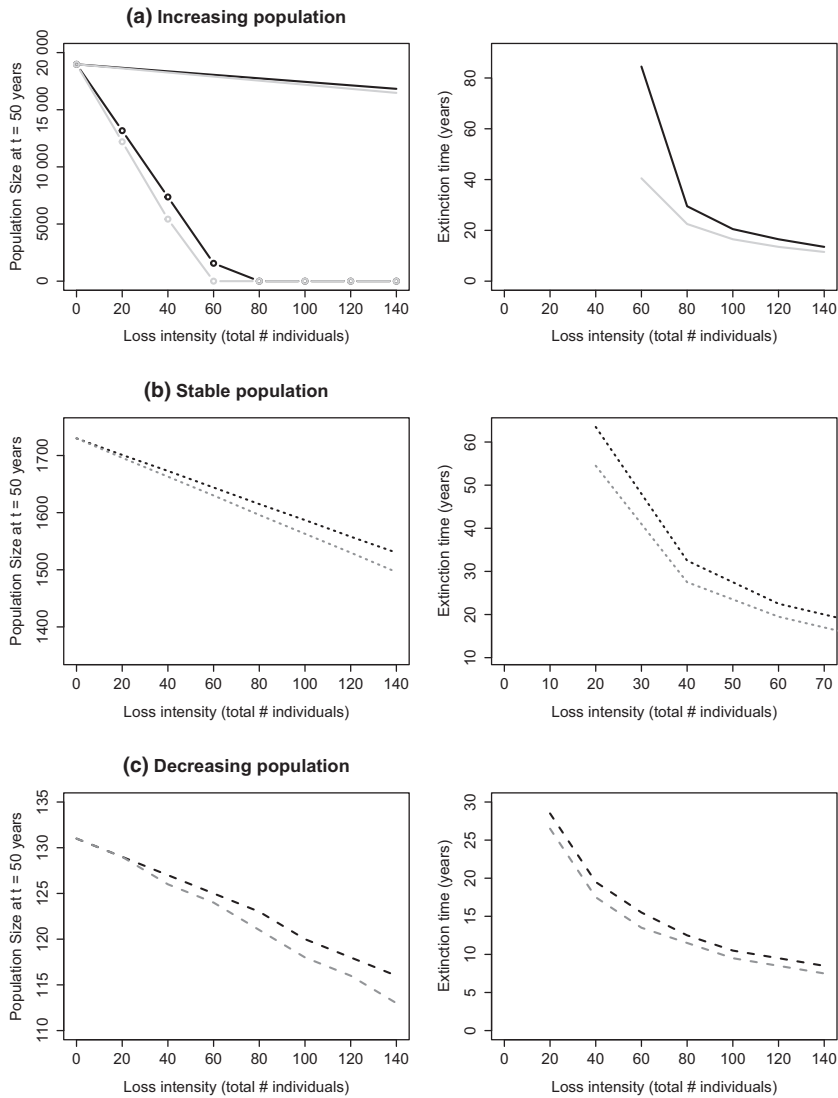

Figure 1 Box turtle population size projected over 50 years, starting with the 2006 population level, for an increasing (solid line; 5% annual increase), a stable (dotted line; 0% annual growth rate), and a declining (dashed line; 5% annual decline) population.

populations, which appear to be in decline (TTWG [Turtle Taxonomy Working Group], 2014). The lack of mammalian predators, separation from the mainland by 2 km of open seawater bisected by powerful currents, and complete protection for nearly 40 years from most human activities undoubtedly have contributed to the population's unusual growth rate. It is not known how long the population has been on the island. Although the level of genetic heterozygosity (0.641) in Egmont Key's box turtle population suggests a long period of isolation (Hagood, 2009), box turtles were not mentioned in surveys in 1869/1870 and 1904 (Franz *et al.*, 1992).

Assuming the population growth rate never changed and that the population started with 10 individuals, it would take between 85 and 90 years to reach the 700 individuals estimated in 1991. This could suggest a founder population colonizing *c.* 1901–1906 during the peak of military occupation of the island during the Fort Dade era, and possibly after the 1904 survey. Box turtles could have been transported to Egmont Key as a result of human activity, or they may have been there all along but gone unreported. After all, Egmont Key is of Pleistocene continental origin and box turtles have colonized many offshore islands along Florida's west coast. In any case, it appears the population has been relatively undisturbed at least since Fort Dade was decommissioned in 1924. With no substantial removal or mortality other than occasional avian predation or storm-related overwash, the population became large and continued to increase through 2006.

Mainland box turtle populations are subject to many forms of disturbances that may or may not result in substantial mortality. Disturbances may be rare over an extended period of time (e.g. catastrophic fires, floods, direct strikes by severe storms, one-time collections by turtle traders) or chronic (e.g. continuous take from a population, decreasing available

Figure 2 Population size projected at 50 years (left panel) and time at complete extinction (right panel) for both a post-breeding (black lines) and pre-breeding (gray lines) removal scenarios in all three cases of increasing (a; solid lines), stable (b; dotted lines), and declining (c; dashed lines) populations. In the case of an increasing population, population size at 50 years could be projected for both a one-time removal event (solid lines) and a chronic (marked lines) removal whereas it could only be projected for a one-time event in the case of a decreasing or stable population.

habitat, periodic low-fuel prescribed fire, exposure to sub-lethal levels of toxic substances, disease, interference by human activity) (e.g. Hall *et al.*, 1999; Rossell *et al.*, 2002; Johnson *et al.*, 2008; Nazdrowicz, Bowman & Roth, 2008; Platt, Liu & Borg, 2010; Currylow *et al.*, 2012; Howey & Roosenburg, 2013; Jergenson *et al.*, 2014; Kiester & Willey, 2015). Some of these impacts (e.g. disease) may be rare events or episodic depending on time scale. On Egmont Key, disturbances since the decommissioning of Fort Dade in 1924 have resulted from passing storm-related overwash, increasing tourism that has altered habitats and possibly led to sporadic take, occasional fires, and an attempt to control the invasion of exotic species through massive cutting and

chemically-based control methods (Dodd *et al.*, 2012). All may be classified as short-term and episodic, and none of these sources appears to have had long-term effects through 2006, possibly because the box turtles were able to move to unaffected portions of the island without substantial mortality (Dodd *et al.*, 2006, 2012).

That is not to say that Egmont Key is immune from catastrophic events. Although no significant declines resulted from impacts from the March 1993 'Storm of the Century' and repeated hurricanes in 2004 and 2005 that skirted the Tampa Bay Region, catastrophic storms have caused severe damage to the island historically, including one in 1848 that knocked the lighthouse off its foundation (Thompson &

Thompson, 2012). There has not been a direct hit by a major hurricane to the Tampa area since 1921 (a storm that caused a storm surge of 3–3.5 m), a time after which corresponded to a period of high growth rates in the box turtle population. The population thus could be vulnerable to a severe catastrophic storm that washed over the entire island, an event from which recovery would take decades.

The results of our simulations suggest that there are important differences as to whether disturbances are rare events or occur repeatedly through time. Assuming the population growth rate continues at 5% and that the demographic parameters we observed remain constant, our models suggest that even substantial mortality due to a rare disturbance event would likely have no effect on the population over a 50-year time span. The population would probably persist if the population growth rate decreased following a disturbance; abundance would remain similar to that at the advent of the disturbance (0% growth rate) or be greatly reduced (5% growth rate decrease), even after 50 years. Box turtle populations thus may be resilient to rare disturbances that result in high mortality/removal as long as the population growth rate is increasing or stable and the population is initially relatively large. These findings are similar to those of Kuo & Janzen (2004) who suggested that despite a high adult survivorship and sufficient recruitment into the population, Ornate Box Turtles in a fragmented and isolated population needed a large population in order to maintain genetic diversity and persist through time.

The results change under a chronic disturbance scenario. Chronic disturbances resulting in even modest annual (<56 individuals, or 3.8% of our initial model population) removal on the 120-ha island would negatively impact the population even if the high population growth rate was maintained. This occurs because the percentage of the population removed increases in subsequent years, even as the number removed remains constant. If population growth rates were only stable or decreasing by 5%, the population quickly declines to extinction within 50 years under both scenarios. As our results demonstrate, more frequent or intensive removal of individuals would lead to almost immediate extirpation. Thus, even a relatively large population of box turtles with high survivorship and recruitment is vulnerable to individual removal (i.e. mortality) when subject to chronic disturbances, especially since recruitment is sensitive to the loss of adults (Bowen, Colbert & Janzen, 2004; Converse, Iverson & Savidge, 2005). Chronic disturbances from a variety of sources may deplete a population, from which it cannot quickly recover even with high individual survivorship. If and when the disturbances ceased, a small population might recover given enough time (mathematically, at least), but even then biological recovery might be prevented by the inability of survivors to find mates or through genetic depression due to low population size (Kuo & Janzen, 2004).

Not unexpectedly perhaps, the timing of disturbances is important when assessing their long and short-term effects. When disturbances impact a population prior to reproduction, they are likely to have more effects on populations than after the egg deposition season. This occurs because one of more season of reproduction is either eliminated or severely reduced, thus impacting subsequent recruitment, sex ratios, and time to maturity (Dodd & Dreslik, 2008). If the disturbances are rare, box turtles tend to adjust their individual growth rates and populations appear to recover quickly as long as survivorship is unaffected (Dodd & Dreslik, 2008). It is likely that chronic stressors affecting turtles immediately prior to or during egg deposition and hatchling would be far more critical to persistence than rare disturbances. Examples of such chronic disturbances include mortality as females cross roads searching for nest sites, early summer plowing and mowing of fields and grasslands, and warm-season timber harvest.

Most box turtle populations, and indeed most terrestrial chelonian populations, have not had the advantages of Egmont Key's protection from anthropogenic stresses over the last 100 years. Turtle populations are increasingly fragmented and unprotected, especially on private lands, and many populations likely are already depleted, relictual, and subject to chronic disturbances, such as flooding, take for pets, predation from subsidized and domestic predators, road mortality, habitat alteration and agricultural activity (Marchand & Litvaitis, 2004; Steen & Gibbs, 2004; Steen et al., 2006, 2012; Freedberg, Lee & Pappas, 2011; Reid & Peery, 2014). Even on 'protected' lands, box turtles are sometimes treated as common species and thus not considered during planning for tourism, timber removal, herbicide application, prescribed burning or other potentially damaging short- or long-term management activities (Dodd, 2005, 2006; Fagundes, Vogt & De Marco Júnior, 2016). Human-caused disturbances can have consequential effects without causing direct mortality, such as by altering behaviour in response to a changed thermal environment (Currylow et al., 2012), which presumably also affect survivorship, recruitment and population size. These activities are generally not one-time disturbances, especially for a turtle that may live many decades, but occur repeatedly and in-combination often over relatively short time spans.

Long-lived turtles appear to be in a precarious position in order to maintain populations and persist in time. Because chelonians live over long periods of time in historically stable environments, they and likely other long-lived species have evolved demographic parameters, particularly high adult survivorship and low but steady recruitment, which have little resilience to chronic and multiple disturbances, especially in fragmented environments. If a severe disturbance occurred >10 000 years BP, for example, populations would recover either slowly through the decades of an individual's life span, or they could be supplemented via immigration from adjacent populations. As long as mortality was not too great, high adult survivorship with steady recruitment also could rebuild a population depleted by episodic disturbances. Today, sufficiently large undisturbed habitats allowing for natural recovery are rare. Even in such favourable habitats, box turtles may be sensitive to factors such as climate change that cannot be easily ameliorated (Converse et al., 2005; McCallum, McCallum & Trauth, 2009).

To persist, most long-lived chelonians require high survivorship, steady recruitment, and relatively large (as yet undefined) populations. Habitats must be sufficiently contiguous to provide sources of immigration, should catastrophic events occur. Persistence results from the subtle interplay of environment, demography and longevity. Anything that interferes with this delicate balance jeopardizes a turtle population. In today's landscape where turtles often persist in isolated habitats, chronic disturbances result in population declines even in protected areas (Kiester & Willey, 2015). Our simulations suggest that declines will occur even when favourable demographic parameters prevail unless populations are initially large with steady or increasing growth rates. In small populations, any periodic removal of individuals would result in a decreased probability of population persistence. This may explain why even protected box turtle populations do not appear to recover or do so only very slowly over a period of years or even decades (e.g. Hall *et al.*, 1999; Schwartz, 2000; Henry, 2003; Ferebee & Henry, 2008), despite individual persistence due to longevity. When managing box turtle populations, factors that result in stress must be minimized, particularly those acting recurrently, in multiples, or when populations are small and fragmented. Box turtle populations are extremely sensitive to chronic individual removal from *whatever* source (Converse *et al.*, 2005; this study), a situation that argues against 'sustained' harvest and supports continued statutory prohibitions against commercial take.

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Authors' contribution

C.K.D. conceived and designed the field study, conducted all field research and took all turtle measurements, and wrote sections of the text. V.R. and M.K.O. conducted the statistical analyses and wrote sections of the text.

References

Balazs, G.H. & Chaloupka, M. (2004). Thirty-year recovery trend in the once depleted Hawaiian green turtle stock. *Biol. Conserv.* **117**, 491–498.

Blaney, R.M. (1971). An annotated check list and biogeographic analysis of the insular herpetofauna of the Apalachicola region, Florida. *Herpetologica* **27**, 406–430.

Bowen, K.D., Colbert, P.L. & Janzen, F.J. (2004). Survival and recruitment in a human-impacted population of Ornate Box Turtles, *Terrapene ornata*, with recommendations for conservation and management. *J. Herpetol.* **38**, 562–568.

Brooks, R.J., Brown, G.P. & Galbraith, D.A. (1991). Effects of a sudden increase in natural mortality of adults on a population of the Common Snapping Turtle (*Chelydra serpentina*). *Can. J. Zool.* **69**, 1314–1320.

Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation*. Sunderland: Sinauer Associates.

Chapin, F.S. III, Kellar, A. & Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *Amer. Nat.* **142**, S78–S92.

Congdon, J.D., Dunham, A.F. & Van Loben Sels, R.C. (1993). Delayed sexual maturity and demographics of Blanding's Turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conserv. Biol.* **7**, 826–833.

Congdon, J.D., Dunham, A.F. & Van Loben Sels, R.C. (1994). Demographics of Common Snapping Turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *Amer. Zool.* **34**, 397–408.

Converse, S.J., Iverson, J.B. & Savidge, J.A. (2005). Demographics of an Ornate Box Turtle population experiencing minimal human-induced disturbances. *Ecol. Applic.* **15**, 2171–2179.

Currylow, A.F., MacGowan, B.J. & Williams, R.N. (2012). Short-term forest management effects on a long-lived ectotherm. *PLoS ONE* **7**, e40473.

Dodd, C.K. Jr (1997a). Population structure and the evolution of sexual size dimorphism and sex ratios in an insular population of Florida Box Turtles *Terrapene carolina bauri*. *Can. J. Zool.* **75**, 1495–1507.

Dodd, C.K. Jr (1997b). Clutch size and frequency in Florida Box Turtles (*Terrapene carolina bauri*): implications for conservation. *Chel. Conserv. Biol.* **2**, 370–377.

Dodd, C.K. Jr (2001). *North American box turtles. A natural history*. Norman: University of Oklahoma Press.

Dodd, C.K. Jr (2005). Dilemma of the common species: Florida Box Turtles. *Iguana* **12**, 153–159.

Dodd, C.K. Jr (2006). Remembering 'common' species during restoration: lessons from Egmont Key (Florida). *Restor. Ecol.* **24**, 211–212.

Dodd, C.K. Jr & Dreslik, M.J. (2008). Habitat disturbances differentially affect individual growth rates in a long-lived turtle. *J. Zool. Lond.* **275**, 18–25.

Dodd, C.K. Jr & Griffey, M.L. (2005). The conservation of box turtles on public lands in Florida. In *Amphibians and reptiles. Status and conservation in Florida*: 103–110. Meshaka, W.E. Jr & Babbitt, K.J. (Eds). Malabar: Krieger Publishing.

Dodd, C.K. Jr, Franz, R.F. & Smith, L. (1994). Activity patterns and habitat use of box turtles (*Terrapene carolina bauri*) on a Florida island, with recommendations for management. *Chel. Conserv. Biol.* **1**, 97–106.

Dodd, C.K. Jr, Ozgul, A. & Oli, M.K. (2006). The influence of disturbance events on survival and dispersal rates of Florida Box Turtles. *Ecol. Applic.* **16**, 1936–1944.

Dodd, C.K. Jr, Hyslop, N.L. & Oli, M.K. (2012). The effects of disturbance events on abundance and sex ratios of a terrestrial turtle, *Terrapene bauri*. *Chel. Conserv. Biol.* **11**, 44–49.

Ernst, C.H. & Lovich, J.E. (2009). *Turtles of the United States and Canada*. 2nd edn. Baltimore: The Johns Hopkins University Press.

Fagundes, C.K., Vogt, R.C. & De Marco Júnior, P. (2016). Testing the efficiency of protected areas in the Amazon for conserving freshwater turtles. *Diver. Distrib.* **22**, 123–135.

Famelli, S., Pinheiro, S.C.P., Souza, F.L., Chiaravolloti, R.M. & Bertoluci, J. (2012). Population viability analysis of a long-lived freshwater turtle, *Hydromedusa maximiliani* (Testudines: Chelidae). *Chel. Conserv. Biol.* **11**, 162–169.

Ferebee, K.B. & Henry, P.F.P. (2008). Movements and distribution of *Terrapene carolina* in a large urban area, Rock Creek National Park, Washington, D.C. In *Urban herpetology*: 365–372. Mitchell, J.C., Jung Brown, R.E. & Batholomew, B. (Eds). Salt Lake City: Society for the Study of Amphibians and Reptiles.

Fordham, D.A., Georges, A. & Brook, B.W. (2007). Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia. *J. Anim. Ecol.* **76**, 1231–1243.

Fordham, D.A., Georges, A. & Brook, B.W. (2009). Experimental evidence for density-dependent responses to mortality of snake-necked turtles. *Oecologia* **159**, 271–281.

Franz, R., Dodd, C.K. Jr & Bard, A.M. (1992). The non-marine herpetofauna of Egmont Key, Hillsborough County, Florida. *Florida Scient.* **55**, 179–183.

Freedberg, S., Lee, C. & Pappas, M. (2011). Agricultural practices alter sex ratios in a reptile with environmental sex determination. *Biol. Conserv.* **144**, 1159–1166.

Garber, S.D. & Burger, J. (1995). A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecol. Applic.* **5**, 1151–1162.

Gibbons, J.W. (1987). Why do turtles live so long? *Bioscience* **37**, 262–269.

Graham, T.E. & Hutchison, V.E. (1969). Centenarian box turtles. *Int. Turtle Tortoise Soc. J.* **3**, 25–29.

Hagood, S. (2009). *Genetic differentiation of selected Eastern Box Turtle (Terrapene carolina) populations in fragmented habitats, and a comparison of road-based mortality rates to population size*. Ph.D. dissertation, University of Maryland, College Park.

Hailey, A. (2000). The effects of fire and mechanical habitat destruction on survival of the tortoise *Testudo hermanni* in northern Greece. *Biol. Conserv.* **92**, 321–333.

Hall, R.J., Henry, P.F.P. & Bunck, C. (1999). Fifty year trends in a box turtle population in Maryland. *Biol. Conserv.* **88**, 165–172.

Henry, P.F.P. (2003). The Eastern Box Turtle at the Patuxent Wildlife Research Center 1940s to the present: another view. *Exper. Gerontol.* **38**, 773–776.

Heppell, S.S., Crowder, L.B. & Menzel, T.R. (1999). Life table analysis of long-lived marine species with implications for conservation and management. *Amer. Fish. Soc. Symp.* **23**, 137–148.

Heppell, S.S., Heppell, S.A., Read, A.J. & Crowder, L.B. (2005). Effects of fishing on long-lived marine organisms. In *Marine conservation biology: the science of maintaining the sea's biodiversity*: 211–231. Norse, E. & Crowder, L.B. (Eds). Washington: Island Press.

Howey, C.A.F. & Roosenburg, W.M. (2013). Effects of fire on the Eastern Box Turtle (*Terrapene carolina carolina*). *Northeast Nat.* **20**, 493–497.

Jennings, A.H. (2003). Daily and seasonal activity patterns and movements of juvenile box turtles (*Terrapene carolina bauri*) on Egmont Key, Florida. *Chel. Conserv. Biol.* **4**, 578–587.

Jennings, A.H. (2007). Use of habitats and microenvironments by juvenile Florida Box Turtles, *Terrapene carolina bauri*, on Egmont Key. *Herpetologica* **63**, 1–10.

Jergenson, A.M., Miller, D.A.W., Neuman-Lee, L.A., Warner, D.A. & Janzen, F.J. (2014). Swimming against the tide: resilience of a riverine turtle to recurrent extreme environmental events. *Biol. Lett.* **10**, 20130782.

Johnson, A.J., Pessier, A.P., Wellehan, J.F.X., Childress, A., Norton, T.M., Stedman, N.L., Bloom, D.C., Belzer, W., Titus, V.R., Wagner, R. & Brooks, J.W. (2008). Ranavirus infection of free-ranging and captive box turtles and tortoises in the United States. *J. Wildl. Dis.* **44**, 851–863.

Kiester, A.R. & Willey, L.L. (2015). *Terrapene carolina* (Linnaeus 1758) – Eastern Box Turtle, Common Box Turtle. *Chel. Res. Monogr.* **5**. (Online DOI:10.3854/crm.5.085.carolina.v1.2015)

Kuo, C.-H. & Janzen, F.J. (2004). Genetic effects of a persistent bottleneck on a natural population of Ornate Box Turtles (*Terrapene ornata*). *Conserv. Gen.* **5**, 425–437.

Laerm, J., Castleberry, N.L., Menzel, M.A., Moulis, R.A., Williamson, G.R., Jensen, J.B., Winn, B. & Harris, M.J. (2000). Biogeography of amphibians and reptiles of the sea islands of Georgia. *Fla. Scient.* **63**, 193–231.

Lambert, M.R.K., Campbell, K.L.I. & Kabigumila, J.D. (1998). On growth and morphometrics of leopard tortoises, *Geochelone pardalis*, in Serengeti National Park, Tanzania, with observations on effects of bushfires and latitudinal

variation in populations of eastern Africa. *Chel. Conserv. Biol.* **3**, 46–57.

Lescroël, A., Dugger, K.M., Ballard, G. & Ainley, D.G. (2009). Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *J. Anim. Ecol.* **78**, 798–806.

Litzgus, J.D. (2006). Sex differences in longevity in the Spotted Turtle (*Clemmys guttata*). *Copeia* **2006**, 281–288.

Lovich, J.E., Ennen, J.R., Madrak, S.V., Loughran, C.L., Meyer, K.P., Arundel, T.R. & Bjurlin, C.D. (2011). Long-term post-fire effects on spatial ecology and reproductive output of female Agassiz's Desert Tortoises (*Gopherus agassizii*) at a wind energy facility near Palm Springs, California, USA. *Fire Ecol.* **7**, 75–87.

Lovich, J.E., Gibbons, J.W. & Agha, M. (2014). Does the timing of attainment of maturity influence sexual size dimorphism and adult sex ratio in turtles? *Biol. J. Linn. Soc.* **112**, 142–149.

Marchand, M.N. & Litvaitis, J.A. (2004). Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conserv. Biol.* **18**, 758–767.

McCallum, M.L., McCallum, J.L. & Trauth, S.E. (2009). Predicted climate change may spark box turtle declines. *Amphibia-Reptilia* **30**, 259–264.

McMahon, C.R., Bester, M.N., Hindell, M.A., Brook, B.W. & Bradshaw, C.J. (2009). Shifting trends: detecting environmentally mediated regulation in long-lived marine vertebrates using time-series data. *Oecologia* **159**, 69–82.

Moll, D. & Moll, E.O. (2004). *The ecology, exploitation, and conservation of river turtles*. Oxford: Oxford University Press.

Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S., Bruna, E.M., Church, D.R., Coulson, T., Doak, D.F. & Forsyth, S. (2008). Longevity can buffer plant and animal populations against changing climatic conditions. *Ecology* **89**, 19–25.

Musick, J.A. (Ed). (1999). *Life in the slow lane: ecology and conservation of long-lived marine animals. American Fisheries Society Symposium 23*. Bethesda: American Fisheries Society.

Nazdrowicz, N.H., Bowman, J.L. & Roth, R.R. (2008). Population ecology of the Eastern Box Turtle in a fragmented landscape. *J. Wildl. Mgmt.* **72**, 745–753.

Pianka, E.R. (1970). On r and K selection. *Amer. Nat.* **104**, 592–597.

Pike, D.A., Pizzatto, L., Pike, B.A. & Shine, R. (2008). Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* **89**, 607–611.

Platt, S.G., Liu, H. & Borg, C.K. (2010). Fire ecology of the Florida Box Turtle (*Terrapene carolina bauri*) in pine rockland forests of the lower Florida Keys. *Nat. Areas J.* **30**, 254–260.

R Development Core Team. (2014). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Available at: http://www.R-project.org.

Reid, B.N. & Peery, M.Z. (2014). Land use patterns skew sex ratios, decrease genetic diversity and trump the effects of recent climate change in an endangered turtle. *Diver. Distrib.* **20**, 1425–1437.

Rossell, C.R. Jr, Rossell, I.M., Orraca, M.M. & Petranka, J.W. (2002). Epizootic disease and high mortality in a population of Eastern Box Turtles. *Herp. Rev.* **33**, 99–101.

Rowe, C.T. (2008). 'The calamity of so long life': life histories, contaminants, and potential emerging threats to long-lived vertebrates. *Bioscience* **58**, 623–631.

Schwartz, E.R. (2000). Update on permanent residency, persistence, and longevity in a 35-year study of a population of Three-toed Box Turtles in Missouri. *Chel. Conserv. Biol.* **3**, 737–738.

Spencer, R.J. & Janzen, F.J. (2010). Demographic consequences of adaptive growth and the ramifications for conservation of long-lived organisms. *Biol. Conserv.* **143**, 1951–1959.

Spencer, R.-J., Janzen, F.J. & Thompson, M.B. (2006). Counterintuitive density-dependent growth in a long-lived vertebrate after removal of nest predators. *Ecology* **87**, 3109–3118.

Steen, D.A. & Gibbs, J.P. (2004). Effects of roads on the structure of freshwater turtle populations. *Conserv. Biol.* **18**, 1143–1148.

Steen, D.A., Aresco, M., Beilke, S.G., Compton, B., Condon, E.P., Dodd, C.K., Forrester, H., Gibbons, J.W., Greene, J.L., Johnson, G. & Langden, T.A. (2006). Relative vulnerability of female turtles to road mortality. *Anim. Conserv.* **9**, 1–5.

Steen, D.A., Gibbs, J.P., Buhlmann, K.A., Carr, J.L., Compton, B.W., Congdon, J.D., Doody, J.S., Godwin, J.C., Holcomb, K.L., Jackson, D.R. & Janzen, F.J. (2012). Terrestrial habitat requirements of nesting freshwater turtles. *Biol. Conserv.* **150**, 121–128.

Stott, J.K. & Davis, R.A. Jr (2003). Geologic development and morphodynamics of Egmont Key, Florida. *Mar. Geol.* **200**, 61–76.

Stubben, C.J. & Milligan, B.G. (2007). Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Software* **22**, 11.

Stubbs, D., Swingland, I.R. & Hailey, A. (1985). The ecology of the Mediterranean Tortoise *Testudo hermanni* in northern Greece (the effects of a catastrophe on population structure and density). *Biol. Conserv.* **31**, 125–152.

Thompson, D.H. & Thompson, C. (2012). *Egmont Key. A history*. Charleston: The History Press.

TTWG [Turtle Taxonomy Working Group]. (2014). Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. *Chel. Res. Monogr.* **5**. (Online DOI:10.3854/crm.5.000. checklist.v7.2014)

Turner, M.G., Collins, S.L., Lugo, A.L., Magnuson, J.J., Rupp, T.R. & Swanson, F.J. (2003). Disturbance dynamics

and ecological response: the contribution of long-term ecological research. *Bioscience* **53**, 46–56.

White, P.S. & Pickett, S.T.A. (1985). Natural disturbance and patch dynamics: an introduction. In *The ecology of natural disturbance and patch dynamics*: 3–13. Pickett, S.T.A. & White, P.S. (Eds). New York: Academic Press.

Wolak, M.E., Gilchrist, G.W., Ruzicka, V.A., Nally, D.M. & Chambers, R. (2010). A contemporary, sex-limited change

in body size of an estuarine turtle in response to commercial fishing. *Conserv. Biol.* **24**, 1268–1277.

Zimmer-Shaffer, S.A., Briggler, J.T. & Millspaugh, J.J. (2014). Modeling the effects of commercial harvest on population growth of river turtles. *Chel. Conserv. Biol.* **13**, 227–236.