The Effects of Disturbance Events on Abundance and Sex Ratios of a Terrestrial Turtle, *Terrapene bauri*

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ABSTRACT. – Disturbances can affect the structure of ecological communities, and their impacts may have consequences for individual species' population dynamics and long-term persistence. Even without catastrophic mortality, survivorship could be reduced following a disturbance, thus leading to population decline. We used a 16-year mark–recapture dataset to determine the effects of catastrophic storms and the cutting of nonindigenous vegetation on the survivorship and abundance of a population of long-lived terrestrial turtles (*Terrapene bauri*). Our results indicate that these habitat disturbances had little long-term effect on abundance. Indeed, the population continued to grow despite severe changes to its habitat, although recapture probabilities decreased through time. Tertiary (adult) sex ratios became more highly skewed temporarily but eventually approached their predisturbance levels. In long-lived box turtles, short-term disturbances may alter growth rates and dispersal tendencies, but they appear to have little long-term effect on abundance as long as initial mortality is not severe and food resources remain available.

KEY WORDS. – Reptilia; Testudines; Emydidae; Florida box turtle; *Terrapene bauri*; disturbance; longevity; abundance; Florida; USA

Stochastic disturbances (White and Pickett 1985) are of particular importance in ecology, despite the difficulty in predicting where and when they will occur (Turner et al. 2003). Both large (e.g., hurricanes) and small (e.g., wind damage in forested habitats) scale disturbances may result in significant changes to surviving communities (Reagan 1991; Tanner et al. 1991; Vandermeer et al. 1996; Woolbright 1996; Greenberg 2001; Vilella and Fogarty 2005), the extent of which is a function of both temporal and spatial scales. Individual species respond in diverse ways to disturbances depending upon their life history and extent of trophic interactions. For example, it has been hypothesized that habitat generalists may be better adapted than specialists in their ability to respond to disturbance, although corroboration has not been forthcoming (Vazquez and Simberloff 2002).

Studies of disturbance have frequently focused on forested, freshwater, and marine habitats (Sousa 1984; Resh et al. 1988; Short and Wyllie-Echeverrias 1996). Stochastic disturbances likely are also important in structuring barrier island communities of the southeastern United States, where severe storms are common (Michener et al. 1997; Davis et al. 2004). The only data on the effects of saline washovers on terrestrial vertebrates is for small lizards (Schoener et al. 2001) and beach mice (Swilling et al. 1998). In these examples, washovers resulted in direct mortality, led to an increased likelihood of emigration, and temporarily altered the life history and demography of the surviving populations. It appears these mobile animals with short generation times can recover quickly as long as minimum ecological requirements are satisfied. This may not be the case with species that have rather different life-history characteristics.

Long-lived vertebrates may be particularly vulnerable to catastrophic events if the physical habitat and food resources are disrupted or if the adult population is seriously reduced. Most studies of disturbances of long-lived species have focused on the effects of chronic perturbations, such as overfishing, on the recovery of imperiled fish, seabirds, and mammals (Musick 1999). The ongoing nature of chronic disturbances makes it difficult to assess the response of these species to episodic disturbance. In many turtles, populations may take a very long time to recover from natural or human-induced perturbations (Brooks et al. 1991; Hall et al. 1999; Balazs and Chaloupka 2004), presumably because turtle life-history characteristics make it difficult to increase survivorship in species that already have relatively high adult survivorship and high mortality as eggs and juveniles. On the other hand, longevity may offer turtles the ability to ''ride out'' disturbances as long as resources remain available and the population is not annihilated.

Previous work on the effects of disturbance events on an insular box turtle population has suggested that, if given the opportunity, turtles will leave the area most affected (Dodd et al. 2006), affirming the so-called evacuation hypothesis (Semlitsch et al. 2008). The growth rates of survivors also changed, likely because of increases in resource abundance following the disturbances, which in turn affected the age at sexual maturity (Dodd and Dreslik 2008). Demographic characteristics (population growth rate, survivorship, recruitment, capture probabilities), however, did not seem to be affected by habitat disturbances (Dodd et al. 2006). In the present study, we used a 16-yr capture–mark–recapture dataset to

examine the long-term effects of two types of simultaneous habitat perturbations on the abundance and adult sex ratio of a Florida box turtle (*Terrapene bauri*) population. Given previous results (Dodd et al. 2006), we hypothesized that overall abundance was unlikely to have been reduced but that the male-biased tertiary sex ratio would become more pronounced.

METHODS

Study Site. — 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 (lat 27°36′04″N, long 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 et al. 1992; Dodd et al. 1994; Stott and Davis 2003; Dodd and Griffey 2005). Historically, the island has been subject to severe periodic erosion, and nearly half of the island, especially on the west and northwestern sides, has disappeared since it was mapped by the Coast and Geodetic Survey in 1875 (Stott and 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 (C.K. Dodd, unpubl. data, 1998–2000). 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.

Study Species. — The Florida box turtle, *T. bauri* (sensu Butler et al. 2011) 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 clutch size = 2, 0–3 clutches per year; Dodd 1997a), high adult and subadult survivorship (> 87%; Dodd et al. 2006), delayed sexual maturity (in Florida, males reach maturity at 8–9 yrs and females at 10–11 yrs; Dodd and

Dreslik 2008), low nest and hatchling survival, and a long life span (> 50 yrs) (Dodd 2001). 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).

Sampling and 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 d. Box turtles were found in all sections of Egmont Key's approximately 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 captured 5662 times in this study. More extensive information is presented elsewhere (Dodd et al. 1994, 2006; Dodd 2001; Dodd and 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 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; Dodd 1997b), and straight-line carapace length (CL) was measured to the nearest millimeter. Turtles were given a unique number by notching the carapace, photographed dorsally for future recognition, and released at point of capture.

Capture–Mark–Recapture (CMR) Analysis. — We used a superpopulation CMR framework to estimate box turtle abundance and to test hypotheses regarding factors influencing population abundance (Schwarz and Arnason 1996, 2011; Williams et al. 2002). This parameterization models a hypothetical superpopulation N (which consists of all animals that would ever hatch in the population) that serves as a source of individuals for the population of interest and the probability that an individual from this superpopulation would enter the population between occasion i and $i + 1$ (b_i; probability of entry). Other parameters that are estimated include apparent survival probability (φ_i) between occasions i and $i + 1$ and the probability of capture (ρ_i) for animals in the population at time i given the animal is alive. Given estimates of N, φ_i, ρ_i, and b_i, estimates of population size are iteratively obtained as a function of survival and recruitment at time $i - 1$ ($B_i = Nb_i$) (Williams et al. 2002; Schwarz and Arnason 2011).

Because the sex of juvenile box turtles cannot be determined reliably, we categorized individuals into three demographic groups for analysis: juveniles were individuals originally captured at a carapace length < 120 mm and not captured again as an adult; males and females were individuals caught originally as either a juvenile or adult; but, if caught as a juvenile, were caught again as an adult and assigned a sex. We tested for the effect of group (sex) and time (year) on model parameters, but sample
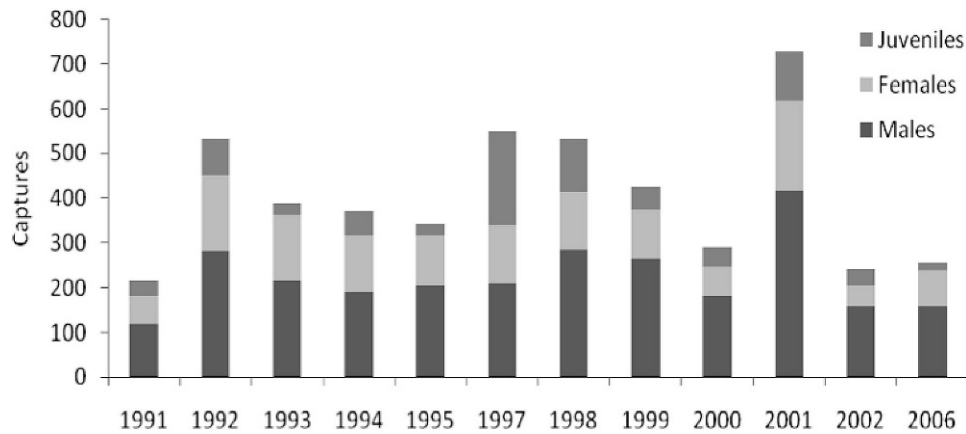
Figure 1. Annual distribution of male, female, and juvenile Florida box turtle (*Terrapene bauri*) captures on Egmont Key, Florida, 1991–2006.

size limited evaluation of additive and interactive effects of these variables. We also examined the effect of the disturbances in 1995–1996 by comparing survival and recapture rates pre- and post-disturbance. Models were implemented with the RMark interface (Laake and Rexstad 2007) to Program MARK (White and Burnham 1999). We used an information-theoretic approach, based on Akaike Information Criterion corrected for small sample size (AIC_c) for model comparison and statistical inferences (Akaike 1973; Burnham and Anderson 2002; Williams et al. 2002). We also calculated model-averaged estimates of survival, recapture probability, and population size to account for model selection uncertainty (Burnham and Anderson 2002).

RESULTS

We used CMR data collected from 2461 box turtles captured from 1991 to 2006 (excluding 1996 and 2003–2005) on Egmont Key. The adult sex ratio was male biased throughout the study and varied temporally, with an average ratio of males to females of 2.06 (range: 1.46–3.27) across the study period (Fig. 1). Mean carapace length at initial capture was 91.3 mm for juveniles, 131.4 mm for females, and 134.6 mm for males.

The most parsimonious model (Table 1, model 1) included an effect of sex on survival and probability of entry into population, with an effect of time on recapture probability; this model received overwhelming support and was separated from competing models by $AIC_c \geq 110$. Survival was lower for juveniles compared to adult males and females, and population size exhibited an increasing trend over time (Fig. 2). Model averaged estimates of annual survival were 0.536 (0.478–0.592, 95% CI) for juveniles, 0.923 (0.911–0.933, 95% CI) for adult males, and 0.911 (0.895–0.924, 95% CI) for adult females. Model averaged estimates of superpopulation size (*N*) were 1718 (1496–1941, 95% CI) for juveniles, 2004 (1924–2083, 95% CI) for males, and 1006 (950–1062, 95% CI) for females. Model averaged recapture rates ranged from a low of 0.164 (0.142–0.189, 95% CI) in 2006 to a maximum of 0.593 (0.539–0.664, 95% CI) in 1992 (Fig. 3).

DISCUSSION

Abundance Estimates. — Box turtles were common and conspicuous on Egmont Key, with estimates of 1000–1200 males, approximately 400 females, and 100–200 juveniles present in 2002. Despite intensive habitat

Table 1. Subset of models from capture–mark–recapture analysis using the superpopulation parameterization of the Jolly-Seber model to test for effects of sex (juvenile, male, female), time (year), and disturbance (pre- and post-1996) on apparent survival (φ), recapture probability (ρ), probability of entry into the population (*b*), and superpopulation (*N*) for Florida box turtles (*Terrapene bauri*), 1991–2006 on Egmont Key, Florida. Because we were interested in estimates of abundance by sex, the superpopulation parameter was constrained to be sex specific (i.e., (*N*[sex]).

| Model no.	Model	No. parameters	ΔAIC_c	AIC_c weight	Log-likelihood
1	φ(sex) ρ(time) *b*(sex)	21	0	1	11,883.95
2	φ(sex) ρ(time) *b*(.)	19	110.17	0	11,998.15
3	φ(.) ρ(time) *b*(sex)	19	315.40	0	12,203.38
4	φ(disturbance) ρ(time) *b*(sex)	20	316.73	0	12,202.69
5	φ(.) ρ(time) *b*(.) *N*(sex)	17	388.06	0	12,280.07
6	φ(disturbance) ρ(time) *b*(.)	18	389.76	0	12,279.76
7	φ(disturbance) ρ(sex) *b*(sex)	11	698.68	0	12,602.77
8	φ(disturbance) ρ(sex) *b*(.)	9	720.81	0	12,628.91
9	φ(sex) ρ(sex) *b*(sex)	12	745.25	0	12,647.32
10	φ(sex) ρ(disturbance) *b*(sex)	11	761.11	0	12,665.2
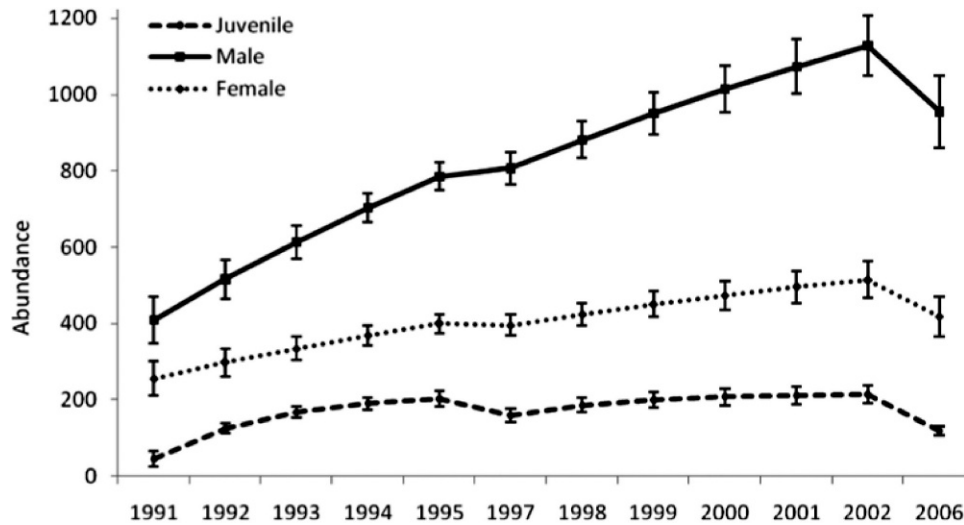
Figure 2. Population abundance over time for juvenile, adult male, and adult female Florida box turtles (*Terrapene bauri*) on Egmont Key, Florida, from 1991–2006. Values are model averaged estimates from the candiate set of models presented in Table 1 ± 95% CI.

perturbations in the mid-1990s, the population continued to grow from 1991–2002. Between 2002 and 2006, population size decreased slightly, perhaps in response to the four intense hurricanes in 2004 when much of the southern and central portions of the island were inundated. Even then, the 2006 estimates were not significantly less than the 2002 estimates. However, recapture probabilities decreased through time.

The reason for continued population growth is not well understood. After the 1995–1996 disturbances, overall population growth rates remained unchanged through 2002 (Dodd et al. 2006), although individual growth rates varied by sex. Male growth rates increased by 19% following the 1995–1996 disturbances, whereas female growth rates decreased by 19% (Dodd and Dreslik 2008). Dodd and Dreslik (2008) hypothesized that food resources may have increased following disturbances, and males grew faster, whereas females put more energy into reproduction. This suggestion appears justified by the documented increase in juvenile recruitment between

1997 and 1999 (Dodd et al. 2006). The basis for an increase in resources is not known.

There are few estimates of box turtle density with which to make comparisons. Langtimm et al. (1996) estimated there were 16.4 turtles/ha on the southern portion of Egmont Key in 1993, similar to the approximate 16 turtles/ha we found throughout the island. This density is similar to densities of mainland populations in Maryland, Missouri, and Tennessee but was much greater than an Indiana population (Dodd 2001). Some differences likely result from the reliability of the methods used to estimate density and differences in time and habitats, but large densities of box turtles may be normal in habitats unaffected by human activity.

Tertiary Sex Ratios. — The tertiary (= adult) sex ratio of box turtles on Egmont Key was skewed toward males throughout the study. From 1991–1995, the ratio was 1.5–1.8 males per female, but from 1999–2002, the ratios became more skewed, from 2.5–3.3 males per female. Survivorship and recruitment rates were similar for males and females (Dodd et al. 2006), therefore, differential mortality cannot explain the male bias. In addition, males, females, and juveniles used habitats similarly (Dodd et al. 1994), and there is no evidence of differential resource availability between sexes or life stages.

Box turtles have temperature-dependent sex determination (TSD), with males produced from cool clutches and females from warm clutches (Ewert and Nelson 1991). On Egmont Key, nesting likely occurs in the moderately cool interior, the only place on the island where deep, organic, and moist soils are found. Much of the island is composed of scattered vegetation in exposed sand that receives intense insolation, to 50°C surface temperature. Female nest site selection could only account for a male-biased sex ratio if females choose not to nest in the widely available exposed sand but only
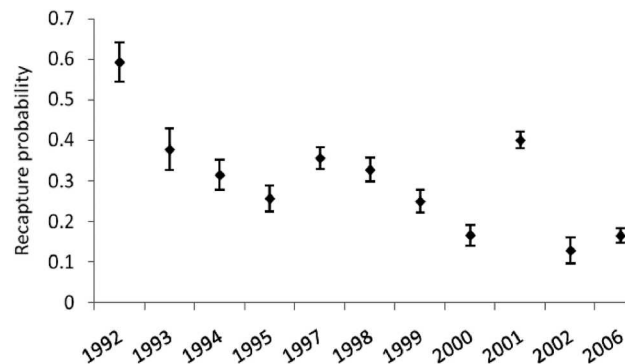
Figure 3. Model averaged estimates (± 95% CI) of temporal differences in probability of recapture for Florida box turtles (*Terrapene bauri*), 1991–2006, on Egmont Key, Florida.

nest in the cool interior. Unfortunately, only one nest has been observed during 16 yrs of study.

Biased sex ratios may not be entirely attributable to nest site choices. Adult sex ratios became even more skewed after the disturbances of 1995–1996. As previously noted, individual growth rates changed after 1996, resulting in a 1-yr decreased time to maturity in males and a 2.5-yr increase in time to maturity in females The subadult stage also increased by 1.5 yrs (Dodd and Dreslik 2008). Changes in growth rates and age at sexual maturity could result in an apparent increase in adult males because they entered the adult population younger than did females (Lovich and Gibbons 1990). In the future, adult sex ratios might return to pre-1996 levels and, indeed, there were 1.98 males per female in 2006, essentially the same ratio (2.06♂:1♀) recorded for the entire study from 1991–2006. For whatever reason, the tertiary sex ratio of box turtles on Egmont Key appears to be a fluctuating statistic rather than a statistic conforming to a 1:1 ideal as in species with genotypic sex determination.

Box turtles on Egmont Key undoubtedly have faced many disturbances on the island since it was first colonized. In addition to storms and recent vegetation changes, the island has a long human history (Stafford 1980). Genetic evidence suggests that box turtles have been on Egmont Key for a very long time (Hagood 2009). Despite substantial habitat changes over the last 150 yrs, the Egmont Key box turtle population was large and even growing throughout much of the 1990s. Survivorship, recruitment, population growth rates, and capture probabilities remained essentially unchanged during much of this study. Box turtles responded to disturbances by moving to areas unaffected by washover and tree cutting (Dodd et al. 2006), following the prediction of the evacuation hypothesis. Adult growth rates were altered (Dodd and Dreslik 2008), and adult sex ratios became even more male biased temporarily because of the increasing disparity in age at sexual maturity between the sexes. Abundance was not affected, and indeed the population even increased, likely until the extreme hurricane events throughout the summer of 2004.

As long as some habitat was unaffected by disturbance-related events, the demography of *T. bauri* on Egmont Key remained relatively unchanged following the two distinct types of disturbances. Longevity essentially allows box turtles and probably other long-lived species to ride out such stochastic short-term disturbance events. Without refuges, long-lived vertebrates may recover only very slowly or not at all, although this has not been well explored.

LITERATURE CITED

AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N. and Csaki, F. (Eds.). Second International Symposium of Information Theory. Akademiai Kiado, Budapest, Hungary, pp. 267–281.

BALAZS, G.H. AND CHALOUPKA, M. 2004. Thirty-year recovery trend in the once depleted Hawaiian green turtle stock. Biological Conservation 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.

BROOKS, R.J., BROWN, G.P., AND GALBRAITH, D.A. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69:1314–1320.

BURNHAM, K.P. AND ANDERSON, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach. Second edition. New York: Springer-Verlag.

BUTLER, J.M., DODD, C.K., JR., ARESCO, M., AND AUSTIN, J.D. 2011. Morphological and molecular evidence indicates that the Gulf Coast box turtle (*Terrapene carolina major*) is not a distinct evolutionary lineage in the Florida Panhandle. Biological Journal of the Linnean Society 102:889–901.

CONGDON, J.D., DUNHAM, A.E., AND VAN LOBEN SELS, R.C. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.

DAVIS, S.E., III, CABLE, J.E., CHILDERS, D.L., CORONADO-MOLINA, C., DAY, J.W., JR., HITTLE, C.D., MADDEN, C.J., REYES, E., RUDNICK, D., AND SKLAR, F. 2004. Importance of storm events in controlling ecosystem structure and function in a Florida Gulf Coast estuary. Journal of Coastal Research 20:1198–1208.

DODD, C.K., JR. 1997a. Clutch size and frequency in Florida box turtles (*Terrapene carolina bauri*): implications for conservation. Chelonian Conservation and Biology 2:370–377.

DODD, C.K., JR. 1997b. Population structure and the evolution of sexual size dimorphism and sex ratios in an insular population of Florida box turtles *Terrapene carolina bauri*. Canadian Journal of Zoology 75:1495–1507.

DODD, C.K., JR. 2001. North American Box Turtles, a Natural History. Norman: University of Oklahoma Press.

DODD, C.K., JR. 2006. Remembering ''common'' species during restoration: lessons from Egmont Key. Restoration Ecology 24:211–212.

DODD, C.K., JR. AND DRESLIK, M.J. 2008. Habitat disturbances differentially affect individual growth rates in a long-lived turtle. Journal of Zoology (London) 275:18–25.

DODD, C.K., JR. AND GRIFFEY, M.L. 2005. The conservation of box turtles on public lands in Florida. In: Meshaka, W.E., Jr.

and Babbitt, K.J. (Eds.). Amphibians and Reptiles, Status and Conservation in Florida. Malabar, FL: Krieger Publishing, pp. 103–110.

DODD, C.K., JR., FRANZ, R.F., AND SMITH, L.L. 1994. Activity patterns and habitat use of box turtles (*Terrapene carolina bauri*) on a Florida island, with recommendations for management. Chelonian Conservation and Biology 1:97–106.

DODD, C.K., JR., OZGUL, A., AND OLI, M.K. 2006. The influence of disturbance events on survival and dispersal rates of Florida box turtles. Ecological Applications 16:1936–1944.

EWERT, M.A. AND NELSON, C.E. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50–69.

FRANZ, R., DODD, C.K., JR., AND BARD, A.M. 1992. The non-marine herpetofauna of Egmont Key, Hillsborough County, Florida. Florida Scientist 55:179–183.

GREENBERG, C.H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management 148:135–144.

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. PhD dissertation, College Park: University of Maryland.

HALL, R.J., HENRY, P.F.P., AND BUNCK, C.M. 1999. Fifty-year trends in a box turtle population in Maryland. Biological Conservation 88:165–172.

JENNINGS, A.H. 2003. Daily and seasonal activity patterns and movements of juvenile box turtles (*Terrapene carolina bauri*) on Egmont Key, Florida. Chelonian Conservation and Biology 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.

LAAKE, J.L. AND REXSTAD, E. 2007. RMark—an alternative approach to building linear models. Appendix C. In: Cooch, E.G. and White, G.C. (Eds.). Program MARK: A Gentle Introduction. http://www.phidot.org/software/mark/docs/book/.

LAERM, J., CASTLEBERRY, N.L., MENZEL, M.A., MOULIS, R.A., WILLIAMSON, K., JENSEN, J.B., WINN, B., AND HARRIS, M.J. 2000. Biogeography of amphibians and reptiles of the sea islands of Georgia. Florida Scientist 63:193–231.

LANGTIMM, C.A., DODD, C.K., JR., AND FRANZ, R. 1996. Estimates of abundance of box turtles (*Terrapene carolina bauri*) on a Florida island. Herpetologica 52:496–504.

LOVICH, J.E. AND GIBBONS, J.W. 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. Oikos 59:126–134.

MICHENER, W.K., BLOOD, E.R., BILDSTEIN, K.L., BRINSON, M.M., AND GARDNER, L.R. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. Ecological Applications 7:770–801.

MUSICK, J.A. (Ed.). 1999. Life in the Slow Lane, Ecology and Conservation of Long-lived Marine Animals. American Fisheries Society Symposium 23.

REAGAN, D.P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rainforest. Biotropica 23:468–474.

RESH, V.H., BROWN, A.V., COVICH, A.P., GURTZ, M.E., LI, H.W., MINSHALL, G.W., REICE, S.R., SHELDON, A.L., WALLACE, J.B., AND WISSMAR, R.C. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455.

SCHOENER, T.W., SPILLER, D.A., AND LOSOS, J.B. 2001. Natural restoration of a species-area relation for a lizard after a hurricane. Science 294:1525–1528.

SCHWARZ, C.J. AND ARNASON, A.N. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. Biometrics 52:860–873.

SCHWARZ, C.J. AND ARNASON, A.N. 2011. Jolly–Seber models in MARK. Chapter 13. In: Cooch, E. and White, G. (Eds.). Program MARK: A Gentle Introduction. http://www.phidot.org/software/mark/docs/book/.

SEMLITSCH, R.D., CONNER, C.A., HOCKING, D.J., RITTENHOUSE, T.A.G., AND HARPER, E.A. 2008. Effects of timber harvesting on pond-breeding amphibian persistence: testing the evacuation hypothesis. Ecological Applications 18:283–289.

SHORT, F.T. AND WYLLIE-ECHEVERRIAS, S. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23:17–27.

SOUSA, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

STAFFORD, J.W. 1980. Egmont Key; sentinel of Tampa Bay. Tampa Bay History 2:15–19.

STOTT, J.K. AND DAVIS, R.A., JR. 2003. Geologic development and morphodynamics of Egmont Key, Florida. Marine Geology 200:61–76.

SWILLING, W.R., JR., WOOTEN, M.C., HOLLER, N.R., AND LYNN, W.J. 1998. Population dynamics of Alabama beach mice (*Peromyscus polionotus ammobates*) following Hurricane Opal. American Midland Naturalist 140:287–298.

TANNER, E.V.J., KAPOS, V., AND HEALEY, J.R. 1991. Hurricane effects on forest ecosystems in the Caribbean. Biotropica 23:513–521.

TURNER, M.G., COLLINS, S.L., LUGO, A.L., MAGNUSON, J.J., RUPP, T.S., AND SWANSON, F.J. 2003. Disturbance dynamics and ecological response: the contribution of long-term ecological research. BioScience 53:46–56.

VANDERMEER, J., BOUCHER, D., PERFECTO, I., AND GRANZOW DE LA CERDA, I. 1996. A theory of disturbance and species diversity: evidence from Nicaragua and Hurricane Joan. Biotropica 28:600–613.

VÁZQUEZ, D.P. AND SIMBERLOFF, D. 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. American Naturalist 159:606–623.

VILELLA, F.J. AND FOGARTY, J.H. 2005. Diversity and abundance of forest frogs (Anura: Leptodactylidae) before and after Hurricane Georges in the Cordillera Central of Puerto Rico. Caribbean Journal of Science 41:157–162.

WHITE, G.C. AND BURNHAM, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Suppl):S120–S138.

WHITE, P.S. AND PICKETT, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A. and White, P.S. (Eds.). The Ecology of Natural Disturbance and Patch Dynamics. New York: Academic Press, pp. 3–13.

WILLIAMS, B.K., NICHOLS, J.D., AND CONROY, M.J. 2002. Analysis and Management of Animal Populations. San Diego, CA: Academic Press.

WOOLBRIGHT, L.L. 1996. Disturbance influences long-term population patterns in the Puerto Rico frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae). Biotropica 28:493–501.