

## THE INFLUENCE OF DISTURBANCE EVENTS ON SURVIVAL AND DISPERSAL RATES OF FLORIDA BOX TURTLES

C. KENNETH DODD, JR.,<sup>1,2,3</sup> ARPAT OZGUL,<sup>2</sup> AND MADAN K. OLI<sup>2</sup>

<sup>1</sup>Florida Integrated Science Center, U.S. Geological Survey, 7920 NW 71st Street, Gainesville, Florida 32653 USA

<sup>2</sup>Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611 USA

**Abstract.** Disturbances have the potential to cause long-term effects to ecosystem structure and function, and they may affect individual species in different ways. Long-lived vertebrates such as turtles may be at risk from such events, inasmuch as their life histories preclude rapid recovery should extensive mortality occur. We applied capture–mark–recapture models to assess disturbance effects on a population of Florida box turtles (*Terrapene carolina bauri*) on Egmont Key, Florida, USA. Near the midpoint of the study, a series of physical disturbances affected the island, from salt water overwash associated with several tropical storms to extensive removal of nonindigenous vegetation. These disturbances allowed us to examine demographic responses of the turtle population and to determine if they affected dispersal throughout the island. Adult survival rates did not vary significantly either between sexes or among years of the study. Survival rates did not vary significantly between juvenile and adult turtles, or among years of the study. Furthermore, neither adult nor juvenile survival rates differed significantly between pre- and post-disturbance. However, dispersal rates varied significantly among the four major study sites, and dispersal rates were higher during the pre-disturbance sampling periods compared to post-disturbance. Our results suggest few long-term effects on the demography of the turtle population. Florida box turtles responded to tropical storms and vegetation control by moving to favorable habitats minimally affected by the disturbances and remaining there. As long as turtles and perhaps other long-lived vertebrates can disperse to non-disturbed habitat, and high levels of mortality do not occur in a population, a long life span may allow them to wait out the impact of disturbance with potentially little effect on long-term population processes.

**Key words:** demography; dispersal; disturbance; Florida box turtle; population growth rate; recruitment; survivorship; *Terrapene carolina bauri*.

### INTRODUCTION

Physical disturbances are important factors affecting ecosystem structure and function and may play a crucial role in the maintenance of biotic diversity. Disturbance events temporarily, at least, alter community composition by creating habitat change in a landscape that otherwise may be structurally uniform as a result of long-term stability. Periodic disturbances alter vegetation structure and composition, which in turn influence animal community composition (Blake and Hoppes 1986, Greenberg and Lanham 2001, Greenberg and Forrest 2003). The effects of disturbances on species and communities are a function of both the temporal and spatial scale of the disturbance; individual species respond in myriad ways to disturbances depending upon their life-history dynamics and extent of trophic interaction.

Both large (e.g., hurricanes) and small (e.g., wind damage in forested habitats) disturbances create new

habitats or refugia which, depending on scale, allow for temporary increases in the abundance of normally rare species (Greenberg 2001), decreases in the abundance of more common species, changes in resource availability (Tanner et al. 1991), and the maintenance of patches of favorable habitats for species persistence. Disturbance events may actually reduce competitive dominance and preserve species diversity (Vandermeer et al. 1996) and can lead to substantial population changes in time (Reagan 1991, Woolbright 1996, Vilella and Fogarty 2005). Thus, the study of disturbance events is of particular importance in ecology, despite the difficulty in predicting where and when disturbances will occur (Turner et al. 2003).

A disturbance is “any relatively discreet event in time that disrupts ecosystem, community, or population structure and changes in resource pools, substrate availability, or physical environment” (White and Pickett 1985). Although studies of disturbance frequently have focused on forested habitats (Dale et al. 2001), disturbance events are likely as important in structuring coastal ecosystems (Michener et al. 1997, Davis et al. 2004), especially when disturbances are common, such as on the coastal barrier islands of the southeastern United States. Aside from small lizards

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<sup>3</sup> E-mail: kdodd@usgs.gov

(Schoener et al. 2001) and beach mice (Swilling et al. 1998), there are few data available on the effects of saline washovers on terrestrial vertebrates inhabiting small or barrier islands.

The Florida box turtle, *Terrapene carolina bauri*, is a terrestrial species often found on barrier islands of the southeastern United States (Blaney 1971, Mitchell and Anderson 1994, Laerm et al. 2000). Box turtles are sedentary omnivores with relatively low fecundity and high adult survivorship, delayed sexual maturity (in Florida, males reach maturity at 5–6 years and females at 7–8 years; Dodd 1997a), low nest and hatchling survival, and a long life span (Dodd 2001). Such life-history traits suggest that box turtles might be sensitive to habitat disturbance resulting from hurricanes or other disturbances, especially if survivorship is depressed (Congdon et al. 1994).

Beginning in 1991, the box turtle population on Egmont Key off the west coast of central Florida was studied during a long-term study on the life history of this potentially declining species (Dodd 2001, Dodd and Griffey 2005). In 1995–1996, the island was affected by severe habitat disturbance from tropical storms and a large-scale attempt to remove nonindigenous vegetation. Here, we report on the effects of these disturbances on survivorship and dispersal among different regions of the island. These results have implications for the survival and conservation of long-lived vertebrates subject to intensive disturbance.

#### MATERIALS AND METHODS

##### *Study site*

Egmont Key is a long, narrow, north–south trending island located at the entrance to 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 island is covered largely by a mixed forest consisting of native palms (*Coccoloba uvifera*) and nonindigenous Brazilian pepper (*Schinus terebinthifolius*) and Australian pine (*Casuarina equisetifolia*). Other vegetation types include sea oats meadows, sisal scrub, lawn grass (at the Tampa Bay Pilot's Association compound and near the lighthouse), and anthropogenically-disturbed areas associated with the historical remnants of Fort Dade (Dodd et al. 1994). The geologic and biotic history of the island in relation to habitat and management are reviewed elsewhere (Franz et al. 1992, Dodd et al. 1994, Stott and Davis 2003, Dodd and 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 the island was mapped by the Coast and Geodetic Survey in 1875 (Department of Environmental Protection 1997, Stott and Davis 2003; aerial photos in Hurley and Mohlman 2000; see Fig. 1). Surges from severe storms in the Gulf of Mexico, whether in winter or

during warm-season hurricanes, cause considerable erosion and sometimes nearly wash over the island, especially in low south and central portions. Prior to extensive human coastal development, sand deposition replaced sediments lost during periodic storm disturbances. However, much of the current erosion is exacerbated by disruption of the south-to-north offshore flow of sand because of the construction of jetties and dredging to protect inlets and channels along the coast south of Tampa Bay. Erosion has been particularly severe during the last century, with nearly 350 m of shoreline retreat occurring during this period. Stott and Davis (2003) suggested that most of the shoreline loss resulted from storm events; the island's present configuration results from extended periods of erosion interspersed by brief periods of sand accretion.

Two major habitat disturbances affected the island beginning in the latter half of 1995 (June through November). Four tropical storms (Allison, 4–5 June; Erin, 2–3 August; Jerry, 25 August; Opal, 4–5 November) passed either directly to the north or west of the island in the Gulf of Mexico. Wave heights (defined as significant wave height in meters calculated as the average of the highest one-third of all of the wave heights during a 20-min sampling period) recorded from NOAA buoy 42036 located northwest of Egmont (28°30'22" N, 84°30'37" W) suggest sufficient disturbance (wave heights of 4.6–5.1 m) as to cause significant overwash from Hurricanes Allison and Erin in 1995 (National Data Buoy Center 2005). In October 1996, Tropical Storm Josephine also pushed storm surges of 1.25 m, resulting in waves of 2 m in height, onto Egmont Key, again inundating the western and southern sections (Stott and Davis 2003). Overwash may have extended in a pattern similar to that resulting from Hurricane Ivan in 2004 (Fig. 2).

The second major habitat disruption involved attempts to kill large stands of Australian pine and Brazilian pepper beginning in 1996. These efforts were carried out primarily in the southern portions of the island, and involved tree-ringing larger trees and cutting branches and stems of the Brazilian pepper. Tree-ringing was supplemented by injecting herbicides directly into the tree base. 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 measured by Hobo temperature and relative humidity dataloggers (Onset Computer, Bourne, Massachusetts, USA); C. K. Dodd, unpublished data). As a result, the habitat structure of large sections of the southern portion of the island, where Langtimm et al. (1996) estimated 14.9–16.4 box turtles/ha, was substantially altered. Beginning in 2000, Australian pines and large peppers on the northern end of the island, an area with high turtle abundance, were injected with Garlon 4 (Dow AgroSciences, Indianapolis, Indiana, USA) in an oil-based surfactant. No tree debris was removed, and tangled branches formed



FIG. 1. Aerial view of the northern section of Egmont Key in an undated photo probably taken in the early to mid-1900s. The area outlined in black has completely washed away; it amounts to nearly one-half of the island that was present in 1875. Photo from the Florida State Archives (Number N046232), Tallahassee, Florida, USA.

nearly impenetrable physical barriers from the ground surface to 4–5 m in height.

In the remainder of this paper, pre-disturbance effects relate to events prior to June 1995 (hurricanes and extensive habitat modification associated with exotic vegetation control), whereas post-disturbance effects refer to events after the winter of 1997. From October 1996 until the hurricane season of 2004, no significant storms are known to have impacted Egmont Key.

#### *Sampling and data collection*

Between 1991 and 2002, one to five visits were made per year to Egmont Key, except in 1996. Surveys ( $N = 33$  sampling periods) lasted from three to five days, with from two to five biologists participating in each survey. Box turtles were found in all sections of Egmont Key's ~120 ha and in 9 of its 10 management units as designated by the Florida Park Service (Fig. 2). As of May 2002, 2477 different box turtles were captured 5384 times. More extensive information on the box turtle study and a physical description of the island are presented elsewhere (Dodd et al. 1994, Dodd 2001).

Box turtles were sampled by visual encounter searches inasmuch as these turtles, even juveniles (Hamilton 2000, Jennings 2003), are conspicuous in the thin leaf litter of the island. Searches initially were concentrated on the southern 36.4 ha of the island (management units 2, 3, and 9) but were extended throughout the island during the course of study. Upon capture, turtles were identified as to sex (males have a concave plastron;

females have a flat plastron) or life-history stage (turtles were considered juveniles if carapace length  $< 120$  mm; Dodd 1997a) and were measured; a variety of habitat and environmental measurements also were taken (Dodd et al. 1994). Turtles were given a unique number by notching the carapace (Cagle 1939), photographed dorsally for future recognition, and released at point of capture.

#### *Capture–mark–recapture (CMR) analysis*

We applied capture–mark–recapture analysis to annual recapture data from the 12-year (1991–2002) study to estimate sex and stage-specific apparent survival, site-specific dispersal, and sex-specific population growth and recruitment rates. Analyses were based on annual CMR data, and captures recorded during a separate study of juveniles were included in the appropriate year (Hamilton 2000, Jennings 2003).

The overall, sex-specific, and state-specific survival and dispersal rates were estimated using the CMR models, which were implemented using Program MARK (White and Burnham 1999). First, we used the Cormack–Jolly–Seber (CJS) model (Lebreton et al. 1992, 1993, Williams et al. 2001) to estimate sex-specific overall apparent survival ( $\phi$ ) and recapture rates ( $\rho$ ), to investigate temporal variation in these rates, and to compare survival rates between pre- and post-disturbance periods. For CJS analyses, data from 1840 adult animals with known sex were used.

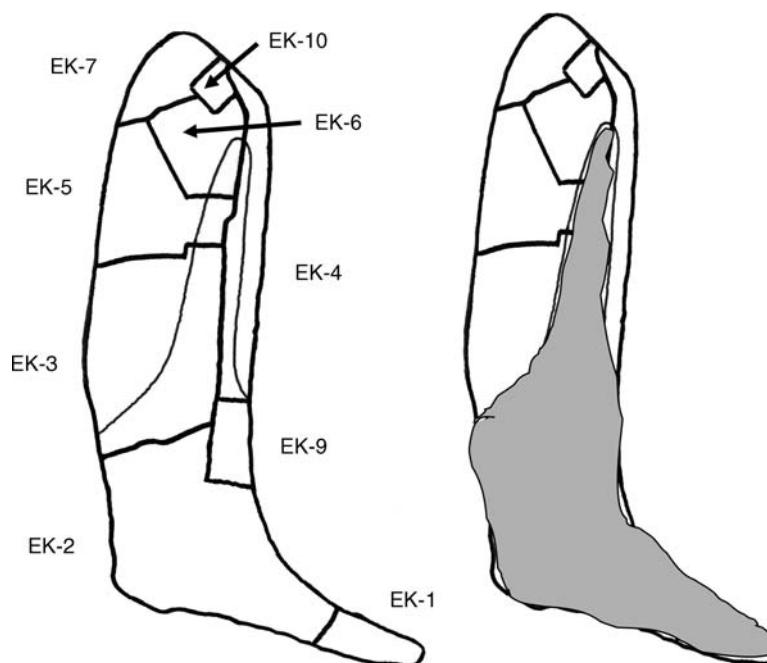


FIG. 2. Location of management units on Egmont Key (left) and extent of seawater washover during Hurricane Ivan in 2004 (shaded, right). The top of the page is north.

We used the multistate CMR model (Hestbeck et al. 1991, Brownie et al. 1993, Williams et al. 2001, Fujiwara and Caswell 2002) to estimate juvenile ( $\phi_{juv}$ ) and adult ( $\phi_{ad}$ ) survival rates, and to investigate temporal variation in these rates. Each of the 2364 turtles used in these analyses was classified either as a juvenile or an adult (Dodd 1997a). The most parsimonious model obtained from the CJS analyses was used as the base model. We also compared juvenile and adult survival rates between the pre- and post-disturbance periods.

We also used the multistate CMR model to estimate the dispersal rates among the four major sites (management units 2, 3, 9, and all other management units combined; Fig. 2), and to test for differences in dispersal rates between males and females, and between juvenile and adult turtles. We compared the dispersal rates between the pre- and post-disturbance periods. Data from 2478 turtles were used for these analyses. The most parsimonious model obtained from the multistate CMR analyses of survival rates was used as the base model for the analyses of dispersal rates. Finally, Pradel's reverse-time CMR model (Pradel 1996) was used to estimate and model the recruitment ( $f$ ) and realized population growth ( $\lambda$ ) rates, and to investigate sex-specific differences and temporal variation in these rates. We also compared the population growth rates between the pre- and post-disturbance periods.

We used Program UCARE V2.02 (Choquet et al. 2003) to test for the goodness of fit of the multistate models, and RELEASE Tests 2+3 (implemented in Program MARK) to test for the goodness of fit of the CJS and Pradel's models. When the overdispersion

parameter ( $\hat{c}$ ) was  $>1$ , we corrected for overdispersion using the calculated  $\hat{c}$ . We used quasi-likelihood adjusted Akaike's Information Criterion, corrected for small sample size, (QAIC<sub>c</sub>) for model comparison, and for the identification of the most parsimonious model from a candidate model set (Burnham and Anderson 2002). Model comparison was based on differences in QAIC<sub>c</sub> values,  $\Delta$ QAIC<sub>c</sub>. We used QAIC<sub>c</sub> weight as a measure of relative support for each model.

## RESULTS

### *Demographic parameters*

The goodness-of-fit test of the general CJS model indicated a slight overdispersion ( $\chi^2 = 161.1$ ,  $df = 84$ ,  $P < 0.001$ ). Thus, we used the calculated value of the overdispersion parameter ( $\hat{c} = 1.92$ ) for parameter estimation, and for quasi-likelihood adjustment for model comparison. The most parsimonious model included time effect, but no sex effect, on recapture rates, and no time or sex effect on survival rates (Table 1, Model 1). Recapture rate estimates ranged from 0.148 (95% CI, 0.117–0.186) to 0.574 (95% CI, 0.451–0.689) among years. Survival rate estimates were 0.886 (95% CI, 0.867–0.905) for males, and 0.871 (95% CI, 0.843–0.895) for females. Furthermore, survival rates did not differ significantly between pre- and post-disturbance periods.

The goodness-of-fit test of the general multistate model for juvenile and adult stages indicated a slight overdispersion ( $\chi^2 = 176.4$ ,  $df = 91$ ,  $P < 0.001$ ). Thus, we used the calculated value of the overdispersion parameter ( $\hat{c} = 1.94$ ) for parameter estimation, and for

TABLE 1. Analysis of the sex-specific and temporal variation in adult survival rates of box turtles (*Terrapene carolina bauri*) using the Cormack-Jolly-Seber model.

Model no.	Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>	np
1	φ(·) ρ(t)	4441.56	0.00	0.305	11
2	φ(pre/post) ρ(t)	4442.17	0.61	0.224	12
3	φ(sex) ρ(t)	4442.68	1.13	0.173	12
4	φ(·) ρ(sex+t)	4442.88	1.32	0.157	12
5	φ(sex+t) ρ(t)	4446.52	4.97	0.025	20
6	φ(t) ρ(t)	4446.90	5.34	0.021	19
7	φ(sex×t) ρ(t)	4452.73	11.18	0.001	27
8	φ(·) ρ(sex×t)	4454.72	13.17	0.000	21
9	φ(·) ρ(·)	4633.60	192.05	0.000	2
10	φ(·) ρ(sex)	4635.57	194.02	0.000	3

Notes: Quasi-likelihood adjusted Akaike's Information Criterion corrected for small sample size (QAIC<sub>c</sub>), differences in QAIC<sub>c</sub> (ΔQAIC<sub>c</sub>), QAIC<sub>c</sub> weights (w<sub>i</sub>), and number of parameters (np) are given for each model. Symbols are: φ, apparent annual survival rate; ρ, annual recapture rate; sex, sex effect; t, = time effect; pre/post, time effect constrained to be pre- and post-hurricane. Interaction effects are indicated by "×" signs. A dot (·) indicates constant value of the parameter.

quasi-likelihood adjustment for model comparison. Survival rates did not vary significantly over time. The estimated survival rates were 0.876 (95% CI, 0.808–0.921) for juveniles, and 0.880 (95% CI, 0.861–0.897) for adults, and did not differ between the two life-history stages (Table 2). Furthermore, neither adult nor juvenile survival rates differed between the pre- and post-disturbance periods.

The goodness-of-fit test of the general multistate model for four sites indicated a slight overdispersion ( $\chi^2 = 355.3$ , df = 263,  $P < 0.001$ ). Thus, we used the calculated value of the overdispersion parameter ( $\hat{c} = 1.35$ ) for parameter estimation, and for quasi-likelihood adjustment for model comparison. For analyses of dispersal rates, we used constant survival {φ(·)} and time-specific recapture {ρ(t)} models because this model structure was identified as the most parsimonious in multistate CMR analyses of survival rates. Dispersal rates varied significantly among the four management units.

Most turtles went back and forth between the mowed lawn and associated brackish swale within the Tampa

Bay Pilot's Association compound (EK-9) and the palm-pepper forest, which bordered all but the northern side of the compound (EK-2). Turtles freely moved across the trail between EK-2 and the palm-pepper forest just north of EK-2; this area (EK-3) provided optimal environmental conditions for box turtles (Dodd et al. 1994) and was essentially contiguous with EK-2. Very little movement occurred between EK-2, 3, or 9 and EK-4, located directly to the north of EK-9. EK-4 consisted mostly of sisal scrub and open habitats providing suboptimal conditions for box turtles (Dodd et al. 1994). Dispersal rates did not significantly vary between males and females or between juveniles and adults (Table 3).

Pre- and post-disturbance dispersal rates differed significantly in all four management units (Table 4). Dispersal rates were generally higher during the pre-disturbance period compared to post-disturbance period (Table 4). After disturbance, dispersal away from a formerly optimal region (EK-2) to adjacent regions increased substantially, and turtles decreased movement into this area. Turtles also decreased dispersal toward a previously favored highly altered management unit (EK-9) after its habitats were modified by saltwater overwash and associated vegetation changes. At the same time, turtles from EK-3, much of which was not affected by severe overwash and habitat structure changes, dispersed less often than they had prior to disturbance events.

The goodness-of-fit test of the general Pradel's model indicated a slight overdispersion ( $\chi^2 = 161.1$ , df = 84,  $P < 0.001$ ). Thus, we used the calculated value of the overdispersion parameter ( $\hat{c} = 1.92$ ) for parameter estimation, and for quasi-likelihood adjustment for model comparison. For the analyses of realized population growth rates, we used constant survival {φ(·)} and time-specific recapture {ρ(t)}, because this model structure was identified as the most parsimonious in CJS analyses. The most parsimonious model indicated a time effect on the realized population growth rate, λ (Table 5, Model 1). Neither realized population growth nor recruitment rates differed between sexes (Table 5) or between pre- and post-disturbance periods (Fig. 3, Table 5).

TABLE 2. Analysis of stage-specific and temporal variation in survival rates of box turtles, using the multistate capture-mark-recapture model.

Model no.	Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>	np
1	φ <sub>juv</sub> (t) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (·) ρ <sub>ad</sub> (t) ψ(t)	5382.29	0.00	0.412	28
2	φ <sub>juv=ad</sub> (·) ρ <sub>juv</sub> (·) ρ <sub>ad</sub> (t) ψ(t) †	5382.44	0.15	0.382	21
3	φ <sub>juv</sub> (·) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (·) ρ <sub>ad</sub> (t) ψ(t)	5384.44	2.15	0.140	22
4	φ <sub>juv</sub> (pre/post) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (·) ρ <sub>ad</sub> (t) ψ(t)	5386.46	4.17	0.051	23
5	φ <sub>juv</sub> (·) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (t) ρ <sub>ad</sub> (t) ψ(t)	5389.09	6.80	0.014	31
6	φ <sub>juv</sub> (t) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (·) ρ <sub>ad</sub> (t) ψ(·)	5394.45	12.16	0.001	19
7	φ <sub>juv</sub> (t) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (t) ρ <sub>ad</sub> (t) ψ(t)	5397.88	15.59	0.000	38
8	φ <sub>juv</sub> (·) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (·) ρ <sub>ad</sub> (t) ψ(·)	5402.05	19.76	0.000	14
9	φ <sub>juv</sub> (t) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (t) ρ <sub>ad</sub> (t) ψ(·)	5405.76	23.47	0.000	29
10	φ <sub>juv</sub> (·) φ <sub>ad</sub> (·) ρ <sub>juv</sub> (t) ρ <sub>ad</sub> (t) ψ(·)	5442.37	60.08	0.000	23

Notes: Symbols are: φ<sub>juv</sub>, juvenile survival rate; φ<sub>ad</sub>, adult survival rate; ρ<sub>juv</sub>, juvenile recapture rate; ρ<sub>ad</sub>, adult recapture rate; and ψ, transition rate from juvenile to adult stage. Other symbols are defined in Table 1.

† Juvenile and adult survival rates were constrained to be the same. See Results: Demographic parameters for details.

TABLE 3. Analysis of dispersal rates of box turtles, using the multistate capture–mark–recapture model; constant survival  $\{\phi(\cdot)\}$  and time-specific recapture  $\{\rho(t)\}$  rates were used in all models.

Model no.	Model	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	$w_i$	np
1	$\phi(\cdot) \rho(t) \psi(\text{site} \times \text{pre/post})$	12 176.59	0.00	1.000	35
2	$\phi(\cdot) \rho(t) \psi(\text{site} + \text{pre/post})$	12 264.85	88.25	0.000	24
3	$\phi(\cdot) \rho(t) \psi(\text{site})$	12 276.05	99.46	0.000	23
4	$\phi(\cdot) \rho(t) \psi_{\text{juv}}(\text{site}) \psi_{\text{ad}}(\text{site})$	12 290.31	113.72	0.000	35
5	$\phi(\cdot) \rho(t) \psi_{\text{juv}}(\text{site}) \psi_{\text{m-ad}}(\text{site}) \psi_{\text{f-ad}}(\text{site})$	12 299.60	123.00	0.000	47
6	$\phi(\cdot) \rho(t) \psi(\text{pre/post})$	12 594.38	417.79	0.000	13
7	$\phi(\cdot) \rho(t) \psi(\cdot)$	12 610.31	433.72	0.000	12

Notes: Symbols are:  $\psi$ , overall dispersal rate;  $\psi_{\text{juv}}$ , juvenile dispersal rate;  $\psi_{\text{ad}}$ , adult dispersal rate;  $\psi_{\text{m-ad}}$ , male adult dispersal rate;  $\psi_{\text{f-ad}}$ , female adult dispersal rate; and site, site effect. A “ $\times$ ” denotes interactions, while a “+” denotes additive effects. Other symbols are defined in Table 1.

DISCUSSION

Many turtles are long-lived, with life-history traits that make recovery from population declines difficult (Congdon et al. 1994; see discussion on long-lived vertebrates in Heppell et al. [1999]). Such traits include high adult survivorship, low nest and hatchling survivorship, increased longevity, and delayed sexual maturity. Many turtles oviposit small numbers of eggs (*T. carolina* on Egmont Key have a modal clutch size of 2, and oviposit from 0 to 3 clutches per year; Dodd 1997b), further exacerbating the ability of a population to rebound from a disturbance. It makes little difference if the disturbance is natural or human-created; turtle populations may take decades to recover from short-term declines or even single catastrophic events (Brooks et al. 1991, Hall et al. 1999, Fonesbeck and Dodd 2003).

Egmont Key box turtles faced three possible outcomes resulting from extensive habitat vegetation control and storm-related seawater overwash: they could be killed; they could survive by staying in place; or they could disperse to favorable or unaffected habitats. There was no evidence of mass mortality. Mortality ranged from 4.5% to 13.6% of the turtles recorded during sampling periods from the spring of 1997 to the spring of 1999,

suggesting higher than normal mortality immediately following disturbance; the effects were relatively short-lived, however. The altered texture of shell keratin indicated that some turtles (both living and dead) were exposed to prolonged contact with salt water. Although the position in which a few shells were found suggested the turtles died as a result of overwash, the locations where they were found do not indicate any unusual spatial patterns (C. K. Dodd, unpublished data). While it is possible that some turtles may have been washed off the island, our results do not support extensive long-term disturbance-related mortality.

The Florida box turtle population on Egmont Key was generally stable during the 12-year study despite the disturbances. Although it appears that recruitment increased during the disturbances (Fig. 3), this anomaly may have resulted from biased sampling. Hamilton (2000) conducted separate studies of juvenile activity and behavior, and focused on marking juveniles. Because many of her marked animals were recaptured in subsequent years, we included them in our models in order to investigate long-term patterns; inclusion of these data likely inflated the apparent rate of juvenile recruitment in 1997 and 1998.

The primary response of the box turtle population on Egmont Key to disturbance was to move away from the affected areas to an area with favored habitat that was largely unaffected either by vegetation control or overwash. Prior to disturbance, considerable back and forth movement occurred between management units. Although Table 4 suggests that much movement occurred from EK-3 to EK-2 and from EK-3 and 4 to EK-9, these results were likely due to unequal sampling effort. Where sampling effort was equal (EK-2 and 9), equal rates of movement occurred back and forth between these adjacent areas. The sampling effort was substantially increased in EK-3 and 4 post-disturbance, and the change in movement rates after the disturbances likely reflects an actual change in dispersal.

Prior to disturbance, EK-9 was a favored morning habitat for box turtles, and as many as 70 or more could be captured in an hour. Morning dew settled in droplets on the lawn grass providing moisture, and a sump area provided semi-fresh water. Saltwater overwash substan-

TABLE 4. Dispersal rates (percentage of dispersal events, mean  $\pm$  SE) of box turtles among adjacent management units before and after disturbance events occurring in mid- to late-summer 1995.

Dispersal to:	Percentage of dispersal events from:			
	EK-2	EK-3	EK-9	Other†
Pre-disturbance				
EK-2		23.6 $\pm$ 7.4	15.9 $\pm$ 1.9	0 $\pm$ 0
EK-3	1.8 $\pm$ 0.6		1.1 $\pm$ 0.6	0% $\pm$ 0
EK-9	13.9 $\pm$ 1.5	37.9 $\pm$ 8.4		23.4 $\pm$ 8.1
Others†	0	0	0	
Post-disturbance				
EK-2		3.1 $\pm$ 0.9	6.1 $\pm$ 1	0 $\pm$ 0
EK-3	6.2 $\pm$ 1		3.4 $\pm$ 0.8	2.2 $\pm$ 1
EK-9	9.9 $\pm$ 1.3	6.1 $\pm$ 1.2		1.7 $\pm$ 0.9
Others†	0.1 $\pm$ 0.2	1.7 $\pm$ 0.6	1.1 $\pm$ 0.4	

Note: Mean values and standard errors were estimated using Model 1 in Table 3.

† EK-4, 5, 6, 7, and 10.

TABLE 5. Analysis of the realized population growth rate ( $\lambda$ ) of box turtles on Egmont Key, using Pradel's reverse-time model.

Model no.	Model	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	$w_i$	np
1	$\phi(\cdot) \rho(t) \lambda(\text{sex}+t)$	8839.32	0.00	0.673	22
2	$\phi(\cdot) \rho(t) \lambda(t)$	8840.84	1.52	0.315	21
3	$\phi(\cdot) \rho(t) \lambda(\text{sex} \times t)$	8847.62	8.30	0.011	31
4	$\phi(\cdot) \rho(t) \lambda(\text{sex})$	8853.05	13.74	0.001	14
5	$\phi(\cdot) \rho(t) \lambda(\text{sex} + \text{pre/post})$	8854.60	15.29	0.000	15
6	$\phi(\cdot) \rho(t) \lambda(\text{sex} \times \text{pre/post})$	8855.86	16.54	0.000	16
7	$\phi(\cdot) \rho(t) \lambda(\cdot)$	8857.17	17.85	0.000	13
8	$\phi(\cdot) \rho(t) \lambda(\text{pre/post})$	8858.63	19.31	0.000	14

Notes: Constant survival  $\{\phi(\cdot)\}$  and time-specific recapture  $\{\rho(t)\}$  rates were used in all the models. Other symbols are defined in Tables 1 and 3.

tially changed this area, however, with vegetation dying back and taking on a burned appearance. The sump area no longer held as much water or for as long, and captures dropped to 5–10 turtles in a “good” morning’s post-disturbance collection. As habitats also became less favorable in adjacent unit EK-2, dispersal back to EK-2 from EK-9 also became less common. As time went on, dispersal decreased dramatically among all management units (Table 4).

Substantial vegetation changes occurred in EK-2, when nearly all of the tall trees were cut down, the habitat was opened and cleared, and dense stands of canopied Brazilian pepper were left as tangled masses of leafless sticks. Much of the dispersal of EK-2’s resident box turtles likely occurred as the habitat changed over 1–3 years rather than in a single short time period. Box turtles became less prone to move to now mostly unfavorable habitat in EK-9, but instead crossed a

narrow dirt trail to EK-3 to the north. EK-3 retained its dense canopy with its open understory and ground surface with deep organic soil pockets, and was mostly unaffected by saltwater overwash.

After Tropical Storm Josephine in October 1996, no storms are known to have seriously impacted Egmont Key until the 2004 summer season, when four major storms crossed Florida. The impact on Egmont Key’s box turtle population from these devastating storms is unknown, although mortality occurred (Florida Department of Environmental Protection, *personal communication*). Our results predict that there will be a slight decrease in survivorship and population growth rate, but that the population may recover in <10 years, assuming there are no more catastrophic events.

Both Brazilian pepper and Australian pine were resprouting throughout EK-2 as of the summer of 2002. In the event of no further vegetation control, it is likely

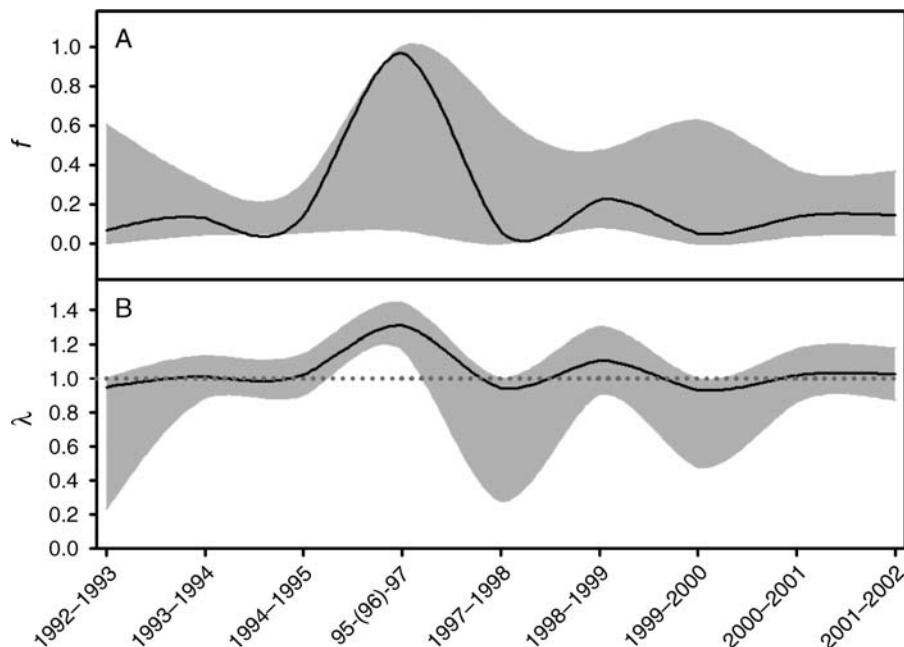


FIG. 3. Temporal variation in the (A) recruitment rate ( $f$ ), and (B) realized population growth rate ( $\lambda$ ) of the box turtle *Terrapene carolina bauri* on Egmont Key, Florida. Mean values (solid line) and 95% confidence intervals (gray shade) were estimated using Model 2 in Table 5. On the x-axis 95-(96)-97 refers to the realized population growth rate between 1995 and 1997, given that no data were collected in 1996.

that the forest on the south end of Egmont Key will again attain its pre-control vegetation structure. We predict that box turtles will increase in numbers in the area as habitat becomes more favorable. Both natural and human-caused events will continue to play major roles in structuring the box turtle population on Egmont Key. As long as there are favorable habitats into which individuals can disperse during disturbances, and as long as the island remains intact and is managed for wildlife (see Dodd and Griffey 2005), box turtles are likely to remain an important component of the island's ecosystem. Our conclusions, however, assume that disturbances do not result in permanent losses of a major portion of the population, particularly breeding adults, through mortality.

Many species may be subject to transient disturbance effects, such as hurricanes, where species-specific responses are modulated by life-history characteristics. Species characterized by early maturity, high fecundity, and short generation times have fast population turnover rates. Because of fast population turnover rates, such species (e.g., Swilling et al. 1998, Greenberg and Miller 2004) may recover from disturbance-caused declines in population size more quickly than species with late maturity, low fecundity, and long generation times. In contrast, long-term persistence of species with slow population turnover may depend on behavioral responses to avoid the aftereffects of disturbance. Our study showed that where habitat is heterogeneous, individuals may respond to disturbances by relocating to unaffected areas serving as refugia. Therefore, habitat heterogeneity and access to refugia may play important roles in long-term persistence of species with slow population turnover rates. Monitoring needs to proceed for many years to assess demographic responses to disturbance.

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