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Sex-biased dispersal and natal philopatry in the diamondback terrapin, *Malaclemys terrapin*

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Abstract

Nesting ecology and population studies indicate that diamondback terrapins (*Malaclemys terrapin*) exhibit nest site fidelity and high habitat fidelity. However, genetic studies indicate high levels of gene flow. Because dispersal affects the genetics and population dynamics of a species, we used six highly polymorphic microsatellite markers to investigate sex-biased dispersal and natal philopatry of *M. terrapin* in Barnegat Bay, NJ. We compared results of spatial autocorrelation analysis, assignment methods and Wright's F_{ST} estimators to a mark–recapture analysis. Mark–recapture analysis over a 4-year period indicated that most individuals have relatively small home ranges (<2 km), with mature females displaying greater home ranges than males. Goodness of fit analysis of our mark–recapture study indicated that some juvenile males were likely transient individuals moving through our study location. Mean assignment indices and first-generation migrant tests indicated that mature males were more prone to disperse than mature females, but first-generation migrant tests indicated that *per capita* there are more female than male dispersers. Thus, the relative importance of males and females on gene flow in terrapin populations may change in relation to population sex ratios. Spatial autocorrelation analysis indicated that mature females exhibited natal philopatry to nesting beaches, but first-generation migrant tests indicated that a small number of females failed to nest on natal beaches. Finally, we discuss the important conservation implications of male-biased dispersal and natal philopatry in the diamondback terrapin.

Keywords: assignment tests, diamondback terrapin, *Malaclemys terrapin*, microsatellite DNA, natal philopatry, sex-biased dispersal

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Introduction

Dispersal affects the genetics and population dynamics of a species. One important type of dispersal pattern is sex-biased dispersal, in which one sex is philopatric while the other sex disperses away from its natal area (Pusey 1987). Male-biased dispersal is often documented in mammals (Dobson 1982), female-biased dispersal is commonly documented in birds (Greenwood 1980; Clarke *et al.* 1997), and female nest site philopatry is often documented in reptiles and fishes (Schwarzkopf & Brooks 1987; Lindeman 1992; Scribner *et al.* 1993; Lohmann *et al.* 1997; Stewart *et al.* 2003; Brown & Shine 2007). Sex-biased dispersal can be measured using either direct or indirect methods (Slatkin 1985). Direct methods, such as mark–recapture or radio-tracking, have been used for many years and have been useful in identifying the movements of many vertebrates. However, they may fail to detect long-distance or infrequent dispersal (Slatkin 1985). Direct measurements of dispersal also do not always reflect the movement of genes. Dispersal and gene flow are only synonymous if the migrant reproduces effectively in the location where it dispersed (Whitlock & McCauley 1999).

Indirect methods are primarily based on genetic differences in populations and can provide a more complete analysis of sex-biased dispersal. Indirect estimates of effective dispersal (reviewed in Goudet *et al.* 2002; Manel *et al.* 2005; Prugnolle & de Meeus 2002; Slatkin 1985) include measures of genetic differentiation using bi-parentally inherited markers and uniparentally

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inherited markers. Differences in levels of genetic differentiation as measured by genetic markers with different modes of inheritance, such as sex-specific and autosomal nuclear markers, can indicate sex-biased dispersal (Prugnolle & de Meeus 2002). Conclusions based on this method need to be interpreted carefully because differences in mutation rates (Balloux *et al.* 2000) and effective population sizes (Chesser & Baker 1996) can lead to differences in the amount of genetic differentiation, rather than differences in dispersal of the sexes.

Indirect methods that use biparentally inherited markers include assignment methods, relatedness with respect to geographical distance (e.g., Mantel tests or spatial autocorrelation), and comparison of Wright's F_{ST} estimators computed both for males and females. The *F*-statistic estimates (such as F_{ST}) mostly reflect historical dispersal behaviour (Bossart & Prowell 1998), while individual-based statistical techniques such as assignment indices and spatial autocorrelation analyses are more useful for detecting current dispersal behaviour (Peakall *et al.* 2003; Paetkau *et al.* 2004; Double *et al.* 2005).

Positive local spatial genetic structure, in which relatedness between individuals declines with increasing geographical distance, results from restricted dispersal within populations (Peakall *et al.* 2003). The presence of positive local spatial genetic structure can be measured using Mantel tests (Smouse *et al.* 1986) and spatial autocorrelation analysis (Epperson & Li 1996). The combination of microsatellite markers and multivariate spatial autocorrelation methods such as the multilocus, multiallele method of Smouse & Peakall (1999) are very sensitive in detecting unexpected fine-scale genetic structure. Spatial autocorrelation analysis has also been used to detect sex differences in dispersal in males and females in a diverse number of species (Stow *et al.* 2001; Double *et al.* 2005; Neville *et al.* 2006; Temple *et al.* 2006; Dubey *et al.* 2008).

The diamondback terrapin is a sexually dimorphic turtle species that inhabits the coastal brackish estuaries along the Atlantic and Gulf coasts of the United States (Iverson 1992). Nesting ecology and population studies indicate that terrapins exhibit nest site fidelity (Auger 1989; Roosenburg 1996; Mitro 2003) and high fidelity to specific creeks (Gibbons *et al.* 2001) or sections of a river (Roosenburg *et al.* 1999). Mark–recapture studies show male and female terrapins occupying areas within a few metres of their original capture location for up to 16 years (Lovich & Gibbons 1990; Gibbons *et al.* 2001). This time frame is presumed to represent the total lifetime movement in terrapins. The generation time is unknown for this species but related species have generation times of 10 (*Chrysemys picta*; Wilbur 1975) and 37 years (*Emydoidea blandingii*; Congdon *et al.* 1993).

Average yearly home ranges vary from 0.54 to 3.05 km^2 (Spivey 1998; Butler 2002) and average distance moved over a period of 6 days is 750.6 m (range 440–1160 m; Harden *et al.* 2007). Nesting ecology studies indicate that nesting female terrapins return to the same dune area to nest (Burger 1977) and many nest within 203 m of their original nest site over two nesting seasons (Szerlag & McRobert 2007). There are a few occurrences of longer-distance movements in which nesting female terrapins moved 4–10 km roundtrip from marsh areas to nesting areas (Gibbons *et al.* 2001; Butler 2002). It is unknown whether females nest on their natal beaches. Although strong data for site fidelity exist in demography studies, low to no genetic differentiation within eastern North Carolina (Hart 2005), southwestern Florida (Hart 2005), South Carolina (Hauswaldt & Glenn 2005), and central New Jersey (Sheridan 2010) suggest significant gene flow. The objective of this study was to (i) determine whether sex-biased dispersal occurs in the diamondback terrapin; (ii) determine whether natal philopatry occurs in the diamondback terrapin; and (iii) compare genetic methods of measuring dispersal with a mark–recapture analysis.

Methods

Study site and field sampling methods

The Barnegat Bay Estuary is a 70-km-long estuary located along the central coast of New Jersey. We trapped terrapins between June-September in 2006–2009 at several locations (Fig. 1). At Island Beach State Park

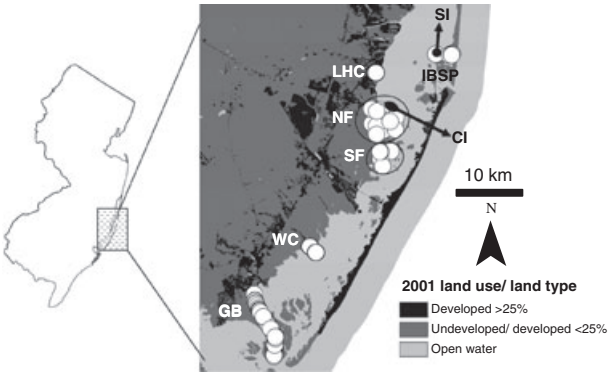

Fig. 1 Map of sampling sites on a 2001 land use map. White circles indicate sampling areas at each location, while the two black circles discriminate between North and South Forsythe. Inset indicates general location of study site on a map of New Jersey. Sampling areas are as follows: Island Beach State Park, Lighthouse Center, North Forsythe, South Forsythe, West Creek, and Great Bay. Locations of Sedge Island and Conklin Island are indicated by black arrows.

(IBSP), Lighthouse Center (LHC), North Forsythe (NF), South Forsythe (SF) and Great Bay (GB) (Fig. 1), we trapped individuals of both sexes in tidal creeks. At Sedge Island (SI), LHC, Conklin Island (CI), West Creek (WC) and GB (Fig. 1), we captured nesting females along dirt embankment alongside roads or on natural nesting beaches during the nesting season. We trapped terrapins using hoop nets, fyke nets, dip nets and hand capture. We individually marked turtles by notching the shell (Cagle 1939) and sexed them (Tucker *et al.* 2001). We took blood samples via the subcarapacial sinus (Hernandez-Divers *et al.* 2002) or the brachial artery (Avery & Vitt 1984). We collected some tail tissue samples from females killed on the road during the nesting season at GB. Samples were collected within 24 h and within several metres of the vehicle encounter. For all captures, we recorded GPS location, mass, straight carapace length, width, height and plastron length.

Direct dispersal analyses

We used capture data from the NF study area exclusively for the direct dispersal analysis because it was the only site that was trapped consecutively for 4 years (2006–2009), contained a large area ($\sim$9 km^2) and was trapped consistently each year from June–September. We briefly compared NF dispersal distances to those reported in the longest-reported mark–recapture analysis for the terrapin (Gibbons *et al.* 2001) and to a smaller data set of individuals recaptured in the SF study area.

We evaluated differences in dispersal between male and female terrapins. Individuals often disperse at the onset of sexual maturity (Handley & Perrin 2007). Thus, analysing all males and females, regardless of sexual maturity, could reduce the ability of the tests to detect sex-biased dispersal (Prugnolle & de Meeus 2002; Lawson Handley & Perrin 2007). Therefore, we classified individuals into four maturity/sex classes: sexually mature males (MM), sexually mature females (MF), juvenile males (JM) and juvenile females (JF). We determined sex on the basis of carapace length, tail thickness and cloacal positioning (Tucker *et al.* 2001). All individuals captured in this study were greater than 90 mm in SCL. At this size, external secondary characteristics are evident, although individuals may not be sexually mature. We considered MF to have a straight carapace length of 140 mm or more (based on minimum sizes of gravid females at our study site). Males greater than 300 g (Roosenburg 1990) were classified as sexually mature. Individuals below these minimum values were considered juveniles.

Before applying analyses to the mark–recapture data set in NF, we assessed how well the capture histories met the necessary assumptions of the classic Cormack–Jolly–Seber (CJS) open population model. (i) Every animal has the same probability of recapture; (ii) every marked animal has an equal probability of survival; (iii) no marks are lost or overlooked; and (iv) sampling is instantaneous and all individuals are released immediately after sampling. Assumption 3 was met because our method of marking turtles with shell notches provides a permanent and unambiguous mark (Cagle 1939). Marks were further verified because mature females were also injected with a passively induced transponder (PIT) tag (Biomark). Assumption 4 was met because we released all individuals at the location of capture within 24 h.

We used goodness of fit testing to determine whether assumptions 1 and 2 were met. We used the program RELEASE 3.0 (Burnham *et al.* 1987) within Program MARK 5.1 (White & Burnham 1999) for the NF study area. RELEASE implements goodness of fit testing (Burnham *et al.* 1987) to test for homogeneity in survival and recapture rates (TEST3) and independence of captures (TEST2). Generally, TEST2 is indicative of a 'trap effect' or other natural phenomena that mimic genuine trap dependence (Pradel 1993). A 'trap effect' could indicate that individuals belonging to different sex or age classes have different probabilities of capture. By testing for different probabilities of subsequent recapture between new individuals and previously identified individuals captured in the same sampling period, TEST3 is indicative of the effects of transients (Burnham *et al.* 1987; Pradel *et al.* 1997). First, we analysed the capture data from NF (2006–2009) without separating the data into maturity/sex classes. If the data failed the overall goodness of fit tests, we proceeded to separate the data into groups on the basis of sex and subsequently into groups based on maturity.

We calculated the average and maximum distances moved by each individual between 2006–2009. We used an ANOVA to determine whether the average distance between recaptures was significantly greater for one maturity/sex class. Any difference in the average distance from the original capture site and recapture sites might be because of a tendency for one sex to have larger home ranges, rather than genuine dispersal (directed movement away from one's natal site). For example, individuals may exhibit seasonal reproductive movements (temporal movement away from one's home range), such as nesting behaviour in females or mate-seeking behaviour in males (Gibbons *et al.* 2001). To assess whether individuals were dispersing further away from their original capture site over time, we tested whether the distance between an individual's original capture and its recapture site(s) significantly increased with the number of days between capture events (*sensu* Dubey *et al.* 2008).

In the NF study area, we also compared the sex ratio of unmarked individuals captured in 2009 with the sex ratio of individuals captured from 2006–2008 to determine whether one maturity/sex class overrepresented the new captures in 2009. We assume that unmarked individuals are of potentially mixed origin (i.e. they may reside in the NF study area but were not captured or they could be immigrants, either permanent or transient, from another area outside the NF). Any sex bias in dispersal might be reflected in the composition of the sample from 2009. For example, if dispersal is primarily by males, then we should find relatively larger numbers of unmarked males in the study area (Dubey *et al.* 2008) in 2009 because dispersing males from outside the study area would be more likely to be found inside the study area than nondispersing females.

DNA laboratory procedures

We preserved blood samples on FTA® cards (Whatman, Part of GE Healthcare). We followed standard manufacturer's instructions for disc removal and modified procedures for FTA purification (Whatman). We punched a 1.2-mm disc (Harris Micro-Punch) from each card using a cutting mat. To prevent cross-contamination between punches, we rinsed the cutting mat with ethanol between each sample. We also punched a disc from an unused FTA® card between each sample to prevent cross-contamination on the micro punch. We rinsed samples once with 50 μL of 70% ethyl alcohol for 5 min, twice with 50 μL of FTA® purification reagent for 5 min and twice with 50 μL of TE buffer (10 mM Tris–HCl, 1 mM EDTA, pH 8.0) for 5 min. We dried sample discs for approximately 10–15 min on a heating block at 50 °C. We conducted PCR analysis within 3 h of disc washing.

We froze tissue samples at −20 °C. We rinsed tissue samples twice with 200 μL of 1× phosphate buffer saline solution (1×, pH 7.4, 11.9 mM phosphates, 137 mM sodium chloride, and 2.7 mM potassium chloride) prior to extraction. We extracted genomic DNA with the DNeasy Tissue kit, following the manufacturer's instructions (QIAGEN).

We designed a 6-microsatellite loci protocol for polymerase chain reaction (PCR) and sequencer load multiplexing. We selected loci from the 27 microsatellite loci that were originally developed for the bog turtle (*Glyptemys muhlenbergii*; King & Julian 2004). King & Julian (2004) screened the 27 loci in *Malaclemys terrapin* and found that 23 successfully amplify and 16 exhibit moderate to high polymorphism. Hart (2005) further screened the 16 loci and chose 12 based on levels of polymorphism and ease of use. Using allele frequencies at each of the 12 loci sampled in Cape May, NJ and Sandy Hook, NJ (Hart 2005), we selected six microsatellite loci for this study based on levels of polymorphism, PI and PI_{sib} (Waits *et al.* 2001). Selected primers and details of the multiplex PCR are shown in Table 1. We ran multiplex PCR products on an ABI 3100 capillary sequencer (Applied Biosystems) together with the internal size standard GENESCAN 500 ROX (Applied Biosystems). We conducted fragment analysis using the software Peak Scanner version 1.0 (Applied Biosystems).

Genetic diversity analyses were conducted using all DNA samples collected from all six study locations (Fig. 1). We used MICROCHECKER 2.2.3 (Oosterhout *et al.* 2004) to detect any genotyping errors, extreme stuttering and null alleles. We calculated null alleles using a Monte Carlo simulation with bootstrap method to generate expected homozygote and heterozygote allele size difference frequencies, which were then compared to the expected Hardy–Weinberg frequencies. We calculated genetic diversity measurements such as mean number of alleles per locus, allele frequencies and gene diversity (Nei 1987) using FSTAT 2.9.3 (Goudet 2001). We used GenALex (Peakall & Smouse 2006) to calculate observed, H_O, and expected, H_E, heterozygosities. We tested for significant deviations from Hardy–Weinberg equilibrium and the presence of linkage disequilibrium using FSTAT 2.9.3 (Goudet 2001), with strict Bonferroni correction applied for multiple comparisons (Rice 1989). We used GenALex (Peakall & Smouse 2006) to calculate probability of identity PI, an estimate of the average probability that two unrelated individuals will by chance have the same multilocus genotype and PI_{sibs}, a probability of identity that takes into account the genetic similarity among siblings (Waits *et al.* 2001).

Genetic analyses of dispersal and natal philopatry

Because direct measurements may not necessarily indicate gene flow, we conducted seven genetic tests for biased dispersal across subpopulations IBSP, NF and SF. These three locations included adequate DNA sampling of each maturity/sex class (Table 2). The distance between these sites is 9.6 km (IBSP-NF), 13.6 km (IBSP-SF) and 4.1 km (NF-SF). The seven indirect tests for biased dispersal included the following: (i) mean corrected assignment index (*m*AIc); (ii) variance of assignment index (*v*AIc); (iii) F_{IS}, a measure of inbreeding within subpopulations relative to the total, (Weir & Cockerham 1984); (iv) F_{ST}, genetic differentiation among subpopulations (Weir & Cockerham 1984); (v) average pairwise relatedness (*r*); (vi) first-generation migrant tests; and (vii) spatial autocorrelation.

We calculated *m*AIc, *v*AIc, F_{IS}, F_{ST} and average relatedness in FSTAT 2.9.3 (Goudet 1995). We determined sta-

Table 1 Characteristics of the 6-microsatellite multiplex kit and measures of gene diversity over all diamondback terrapin samples in Barnegat Bay, NJ (N = 1558)

Loading and PCR plex	Locus	GenBank accession #	Primer concentration (mM)	Size Range (bp)	Label	# of alleles	Ho	He	PIsibs
A	*Gmu*B08	AF517229	0.2	211–241	6-FAM	11	0.829	0.804	0.358
A	*Gmu*D121	AF517252	0.2	124–188	NED	17	0.867	0.876	0.31
A	*Gmu*D62	AF517241	0.25	127–175	HEX	12	0.87	0.794	0.363
B	*Gmu*D87	AF517244	0.2	224–276	6-FAM	14	0.875	0.874	0.32
B	*Gmu*D114	AF517251	0.2	88–124	NED	10	0.696	0.677	0.434
B	*Gmu*D90	AF517247	0.25	111–147	HEX	10	0.81	0.822	0.345

PCR chemistry: 20 μL PCR reactions using 5–15 ng of DNA or 1.2 mm Whatman blood punch, 0.3175 mM dNTPs, 1× GoTaq Flexi Buffer (Promega), 3.75 mM $MgCl_2$, 0.2–0.25 mM primer, 0.5 units of GoTaq polymerase (Promega).
PCR thermocycling: 94 °C for 2 min, 35 cycles of denaturation at 94 °C for 45 s, annealing at 56 °C for 45 s, extension at 72 °C for 2 min. Final extension at 72 °C for 10 min.

Table 2 Samples sizes for which DNA was analyzed for mature females, mature males, juvenile females, and juvenile males from the following sampling locations in Barnegat Bay, NJ: Island Beach State Park (IBSP), North Forsythe (NF), and South Forsythe (SF)

	Mature females	Mature males	Juvenile females	Juvenile males	Total
IBSP	142	8	35	59	244
NF	408	104	173	251	936
SF	55	7	27	31	120
Total	605	119	235	341	1300

tistical significance by comparing actual values to randomized values for 10 000 permutations. Assignment indices followed methods of Paetkau *et al.* (1995), which were later followed by Favre *et al.*(1997) to calculate corrected assignment values (AIc). We expected individuals of the dispersing sex to have a lower *m*AIc, because immigrants have lower AIc values than residents. We expected individuals of the dispersing sex to have a higher *v*AIC because members of the dispersing sex have both immigrants and residents (Goudet *et al.* 2002). The F_{IS} measures how well the genotype frequencies fit Hardy–Weinberg expectations (Hartl & Clark 1997). We expected individuals of the dispersing sex to have a higher F_{IS} (heterozygote deficit) than the philopatric sex because of the Wahlund effect (Goudet *et al.* 2002). The F_{ST} describes the proportion of the total genetic variance among populations (Hartl & Clark 1997). We expected individuals of the philopatric sex to have a higher F_{ST} than the dispersing sex because allele frequencies between subpopulations for individuals of the dispersing sex should be more similar because of effective dispersal (Goudet *et al.* 2002). Average relatedness can be calculated from F_{ST} and F_{IT} through a simple equation ($r = 2\ F_{ST}/(1 + F_{IT})$; Queller & Goodnight 1989 estimator implemented in FSTAT 2.9.3). We expected individuals of the dispersing sex to have a lower average relatedness when compared to the philopatric sex (Prugnolle & de Meeus 2002). We ran analyses with males and females regardless of maturity, mature males and females, and juvenile males and females with three population groupings (IBSP, NF and SF).

First-generation (F_0) migrant tests (GENECLASS 2.0; Piry *et al.* 2004) were used to determine F_0 migrants among mature individuals sampled in IBSP, NF and SF. For migrant detection, we used a likelihood computation with a default frequency for missing alleles of 0.01 and L = L home, the likelihood of the individual genotype within the population where the individual has been sampled (Paetkau *et al.* 1995; Piry *et al.* 2004). We computed the probability that an individual was a resident by using a Monte Carlo resampling algorithm (Paetkau *et al.* 2004) with 10 000 simulated individuals and Type I error rate of 0.05. We tested for differences in the total number and the proportion of MM and MF F_0 migrants.

We used the program GENALEX version 6.2 (Peakall & Smouse 2006) to calculate the multilocus autocorrelation coefficient r among individual genotypes falling within various distance classes. We calculated the r correlation coefficient using two pairwise matrices, one using geographical distances and the other using squared genetic distances (Smouse & Peakall 1999). The r correlation coefficient is similar to Moran's I coefficient, ranges from −1 to +1 and provides a measure of genetic similarity between pairs of individuals falling within each distance class (Peakall *et al.* 2003). To test whether the r correlation coefficient was significantly different from the null hypothesis of no spatial genetic structure, we

performed 1000 random permutations to determine upper and lower confidence intervals for the null hypothesis (Peakall *et al.* 2003).

We presented the correlation coefficient r and associated confidence interval about $r = 0$ as correlograms, which displayed r in relation to distance. We used bin (distance) sizes that represented both the spatial resolution within sampling locations (500, 1000 and 2000 m) and the spatial resolution between sampling locations (4000, 8000, and 14000 m) for the data set comprised of IBSP, NF and SF individuals. Within a given correlogram, we also present the number of pairwise comparisons used at each distance class and the p-values for the one-tailed probabilities of positive and negative spatial genetic structure. We determined distances where the one-tailed probabilities indicated a significance of $P < 0.05$.

To evaluate whether natal philopatry of nesting females occurred, we estimated r (as a function of distance) for nesting females ($N = 132$) from five nesting areas (GB, $n = 84$; WC, $n = 9$; SI, $n = 33$; CI, $n = 12$; LHC, $n = 5$). For some nesting females, we had exact GPS coordinates of the location where the nest was deposited. For gravid females captured on a nesting beach prior to nesting, we assumed that the female would nest at the capture location. We used distance classes that represented both the spatial resolution within sampling locations (5, 500, 1000 and 5000 m) and the spatial resolution between sampling locations (10 000, 20 000 and 36 000 m).

The spatial extent of significant autocorrelation may change when evaluating different distance classes, because the observed patterns are the composite of the true spatial extent and the number of individuals that are evaluated at each distance class (Peakall *et al.* 2003). Therefore, we also evaluated composite graphs containing the results from the first distance bin using different bin sizes. This method evaluated how data pooling affected autocorrelation and allowed us to assess the true extent of detectable positive autocorrelation (Double *et al.* 2005).

Results

Direct dispersal

We marked and released a total of 1277 diamondback terrapins over the 4-year study period (2006–2009) in North Forsythe (JF = 231; MF = 579; JM = 313; MM = 136; and juvenile/no sex, $N = 18$). Recapture rates were relatively low between years, with 11.5% of individuals recaptured at least once in a later year. There were no terrapins initially marked within NF captured at other study locations. However, there were two MFs marked several years prior at the SI nesting location that were recaptured in NF during the 2009 nesting season. The behaviour for these two females could be because of (i) genuine dispersal; or (ii) seasonal reproductive movements. The first female was captured nesting on SI in 2002, 2003 and 2004 and was then recaptured nongravid in a fyke net 8.5 km away in NF in 2009. The second female was captured nesting on SI in 2002, 2005 and 2007 and then captured gravid in a hoop trap 8.1 km away in NF in 2009. Given that 4 and 2 years, respectively, have passed between recaptures and that the second female was gravid in the new location, we suggest that genuine dispersal occurred. Additional recaptures in consecutive years may provide more information.

Output from program RELEASE indicated the goodness of fit tests (TEST2 + TEST3, combined) were significant when the data was pooled for all maturity/sex classes ($P = 0.0013$), indicating heterogeneity in survival and capture probabilities (Burnham *et al.* 1987). Further examination of the results indicated that TEST2 ($P = 0.4291$) and TEST3.SM ($P = 1.0$) were not significant, but TEST3.SR failed the goodness of fit test ($P < 0.001$). When the data were grouped according to sexes, the overall goodness of fit test (TEST2 + TEST3, combined) was not significant for females ($P = 0.21$), but males failed the overall goodness of fit test ($P = 0.012$). Further examination of the results indicated that males significantly failed TEST3.SR ($P < 0.01$). Specifically, males significantly failed TEST3.SR in 2008 ($P < 0.001$). When the male data set was grouped according to maturity, the overall goodness of fit test for mature males was not significant ($P = 0.334$) nor were any of the subtests significant ($P > 0.12$). However, in juvenile males, the contingency table for TEST 3.SR in 2008 ($P = 0.004$) indicated that fewer individuals that were caught, newly marked and released on this occasion were seen again (4.5%) when compared to individuals that were caught, marked before and released on this occasion (33%). Thus, implicating that transients were juvenile males.

In the NF sampling location, the maximum distance recorded was 8508 m by a MF (Table 3). We found significant differences in average distances between immature and mature males and females (ANOVA, $F_{3,145} = 3.66$, $P = 0.014$). Post hoc Tukey–Kramer tests detected that mature females moved greater distances than juvenile males and mature males (at the 0.05 level of significance). The distance between the original capture site and all subsequent capture sites did not increase with time (days) for any maturity/sex class (MF: $F_{1,63} = 2.93$, $P = 0.09$; MM: $F_{1,47} = 0.001$, $P = 0.98$, JF: $F_{1,60} = 0.38$, $P = 0.54$, JM: $F_{1,81} = 1.29$, $P = 0.26$). In the analysis of the relationship between distance and time in MF, we

Table 3 Mean and maximum dispersal distance of diamondback terrapins in Barnegat Bay, NJ that were recaptured at least once, as measured by capture-mark-recapture. Data is categorized by sex and maturity

	N	Mean distance (m)	SE ±1	Maximum distance (m)
Juvenile females	29	301	46	1379
Mature females	45	722	253	8508
Juvenile males	50	148	22	1039
Mature males	25	104	18	780

removed the data points associated with the two MF females that were trapped in both SI and NF. The removal was based on a Cook's distance (Cook 1977) of >1 for both data points (3.1 and 3.9 for the distances of 8.1 and 8.5 km, respectively).

To compare movements in the NF study location to the Gibbons *et al.* 2001 study, we reported movement of individuals without designating maturity. In NF, 32 individuals (21 females and 11 males) were recaptured in another creek or cove (≥500 m straight-line distance). This ratio of 1.9 females per male is not significantly different from the sex ratio of the entire population (1.64:1; $\chi^2 = 0.05$, d.f. = 1, $P = 0.82$). Of the 149 individuals that were recaptured at least once, 21.5% were captured in another creek or cove. In comparison, Gibbons *et al.* 2001 recorded 25 individuals (5.7% of 442 individuals recaptured at least once; 9 females and 16 males) moving between the creeks (≥500 m straight-line distance) of the Kiawah River in South Carolina. The sex ratio of males to females was not different than the sex ratio of the population (1.78 male biased), and many of the individuals that were recaptured more than once were captured within 100 m of their original capture (Gibbons *et al.* 2001).

In the SF sampling location, we captured 169 individuals over the 3 year trapping period (2007–2009). Twenty individuals were recaptured once and five individuals were recaptured twice. Trapping efforts in SF typically occurred from the last week in July to the first week in September and therefore may have missed any movements associated with activities occurring in June and early July (e.g. nesting). Sample sizes of some maturity/sex classes were low (JF = 8, JM = 1, MF = 14, MM = 2); therefore, we pooled the data to determine an average distance (21 m) and maximum distance (227 m). Distance between sampling locations did not increase as a function of time ($F_{1,33} = 0.25$, $P = 0.62$).

Females comprised most of the 247 new captures (53%) in 2009. Juvenile females, juvenile males and mature males comprised 17%, 20% and 10% (respectively) of the new captures in 2009. New captures in 2009 made up 18% of total captures of adult males, 22% of total adult females, 16% of total juvenile males and 18% of total juvenile females. New captures in 2009 did not account for a larger proportion of any one maturity/age class ($\chi^2 = 6.02$, d.f. = 3, $P = 0.11$). New captures can comprise of both unmarked residents and immigrants and it is likely that our resident population in NF is quite large (>4000 C. M. Sheridan, unpublished). Even when a large majority of the resident population has been captured, it might be difficult to distinguish whether differences in sex ratios of new captures are because of environmental sex determination (ESD; Jeyasuria *et al.* 1994), increased mortality or sex-biased dispersal unless hatchling sex ratios and mortality rates are also estimated.

Genetic analysis

We found 74 different alleles in the 1558 individual males, females and juveniles that were genotyped (DNA samples collected 2006–2008 from all trapping locations). The number of alleles per locus ranged from 10 (*Gmu*D114 and *Gmu*D90) to 17 (*Gmu*D121), with a mean of 12.33 alleles per locus. Mean expected heterozygosity (H_E) and observed heterozygosity (H_O) across the study area were 0.808 and 0.825, respectively. There was a low probability of individuals sharing an identical genotype ($PI = 1.4 \times 10^{-08}$ and $PI_{sibs} = 1.9 \times 10^{-03}$). After strict Bonferroni correction (Rice 1989), no departures from Hardy–Weinberg equilibrium were detected at any loci (within all study sites and over all study sites). Possible null alleles were detected for locus *Gmu*D121; however, this only held true for the site GB and not for other sampling sites, or across all sites. The null allele frequency at the *Gmu*D121 locus in GB samples was 0.041 (Chakraborty *et al.* 1992). The lack of departures from Hardy–Weinberg equilibrium indicated the effect of possible null alleles in *Gmu*D121 was limited. Therefore, we included all loci in our data set. No linkage disequilibrium was detected for any pair of loci at any sampling site after strict Bonferroni correction [$a = 0.05$, $k = 90$, $P < 0.001$; (Rice 1989)].

When testing for sex-biased dispersal among all males and females genotyped in NF, SF and IBSP, we found no significant sex-biased dispersal (Table 4a). There was male-biased dispersal when we limited the analysis to mature males and mature females (Table 4b). Mean assignment index was lower for males than females (Table 4b). The variance of assignment index, F_{ST}, F_{IS} and average pairwise relatedness did not differ in mature males and females (Table 4b). There was no sex-biased dispersal among juvenile males and juvenile females (Table 4c).

Table 4a–c Mean assignment (*m*AIC), variance assignment (*v*AIC), *F*-statistics and relatedness (*r*) for each sex (4a, all individuals; 4b, mature individuals; 4c, juvenile individuals). Significance (*P*) was assessed using the randomisation method of Goudet *et al.* (2002). Values in bold indicate $P < 0.05$

		*m*AIC	*v*AIC	F_{ST}	F_{IS}	*r*
a	Males	0.042	5.924	0.002	−0.015	0.004
	Females	−0.024	5.756	0.0001	−0.029	0.0001
	Overall	–	–	0.001	−0.024	0.001
	P	0.683	0.408	0.927	0.061	0.925
b	Males ≥ 300 g	−0.365	5.723	0.004	−0.020	0.008
	Females ≥ 140 mm	0.072	5.517	0.002	−0.028	0.005
	Overall	–	–	0.002	−0.026	0.004
	P	**0.026**	0.261	0.638	0.301	0.636
c	Males < 300 g	0.145	6.130	0.004	−0.019	0.007
	Females < 140 mm	−0.210	6.465	0.002	−0.036	0.004
	Overall	–	–	0.003	−0.026	0.005
	P	0.071	0.336	0.240	0.881	0.245

First-generation assignment tests ($\alpha = 0.05$; GENECLASS 2.0) of mature individuals identified a total of 32 individuals as F_0 migrants (10 MM and 22 MF). Ten F_0 migrants were captured in IBSP (6.7% of 150 captures), six of which were assigned to NF, two to SF and two were home-assigned. A home-assigned migrant indicates that this individual was genetically closer to its population of capture than to other sampled populations. Eighteen F_0 migrants were captured in NF (3.5% of 512 captures), eight of which were assigned to SF, three to IBSP and seven were home-assigned. Four F_0 migrants were captured in SF (6.5% of 62 captures), three of which were assigned to NF and one was home-assigned. Overall, 4.4% (32 of 724 captures) were identified as F_0 migrants. The proportion of individuals assigned as F_0 migrants did not differ between the three trapping locations ($\chi^2 = 3.39$, d.f. = 2, $P = 0.18$). A larger number of MF were identified as F_0 migrants when compared to MM ($\chi^2 = 4.5$, d.f. = 1, $P = 0.034$). Our ability to determine the overall tendency for one sex to disperse more than another could be affected by the larger number of MF (605 vs. 119 MM, $P < 0.001$). Overall, the proportion of immigrants vs. residents was significantly greater for MM (8.4%) than for MF (3.6%; $\chi^2 = 5.33$, d.f. = 1, $P = 0.021$).

Spatial autocorrelation analysis of all individuals genotyped from IBSP, NFOR and SFOR ($N = 1300$) showed significantly positive *r* values within the 1000–2000 m distance class and significantly negative r values within the 8000–14 000 m distance class (Fig. 2a). Similar results were found if the analysis was restricted to mature females (Fig. 2b). When the analysis was restricted to mature males only (Fig. 2c), juvenile males only (not shown) and juvenile females only (not shown), there was no significant positive autocorrelation. Analysis of all nesting females ($N = 143$) showed significant positive *r* values within the 0–50 m distance class (Fig. 2d). When evaluating the effect of bin size, mature females had significant positive *r* values for the 0–2000, 0–5000 and 0–7500 m bins sizes, and the *x*-intercept for the 0–7500 m bin size (i.e. maximum extent of spatial autocorrelation) was 10 201 m (Fig. 3a). Nesting females had significant positive *r* values for the 0–5, 0–10, 0–50, 0–100 and 0–150 m bin sizes, and the *x*-intercept for the 0–150 m bin size was 201 m (Fig. 3c).

Discussion

The contrast between the direct and indirect measures in this study highlights the limitations of detecting dispersal using the direct method of mark–recapture (Slatkin 1985); additional direct methods, such as radio- or sonic-tracking may augment the mark–recapture data. Our mark–recapture study indicated that individuals move relatively small distances (<2000 m; Table 3, with the exception of 2 MF moving distances greater than 8 km from a nesting beach to a marsh area). The movements support studies showing fidelity of terrapins to marsh areas (Roosenburg *et al.* 1999; Gibbons *et al.* 2001; Harden *et al.* 2007); however, the autocorrelation analysis and other genetic measures of sex-biased dispersal (e.g. *F*-statistics) indicate high levels of gene flow and limited genetic structure. Because the distance moved was not correlated with time in any of the maturity/sex classes, we conclude that direct measurements indicate that mature females have greater home range sizes than males (Table 3). Greater home range sizes measured in mature females were likely due to seasonal reproductive movements in which females make temporal forays away from foraging areas to nesting areas. Although our goodness of fit analysis indicated that some juvenile males were likely transient individuals moving through the NF location, our comparisons of the sex ratios individuals did not indicate a larger proportion of any single sex in 2009.

The frequency of movements between creeks in NF was much higher in comparison with the Gibbons *et al.* 2001 study. We hypothesize that there are differences between the two populations in one or several of the following: (i) dispersal related to reproduction (e.g. mate seeking and nesting); (ii) dispersal related to hibernation; and (iii) dispersal related to habitat requirements (e.g. foraging behaviour or habitat suitability; Gibbons *et al.* 2001). Indeed, one of the creeks in the Gibbons *et al.* 2001 study did have a much higher frequency of movement when compared to the average of all the creeks (24.5% in Terrapin Creek). The higher frequency was attributed to an increase boating and

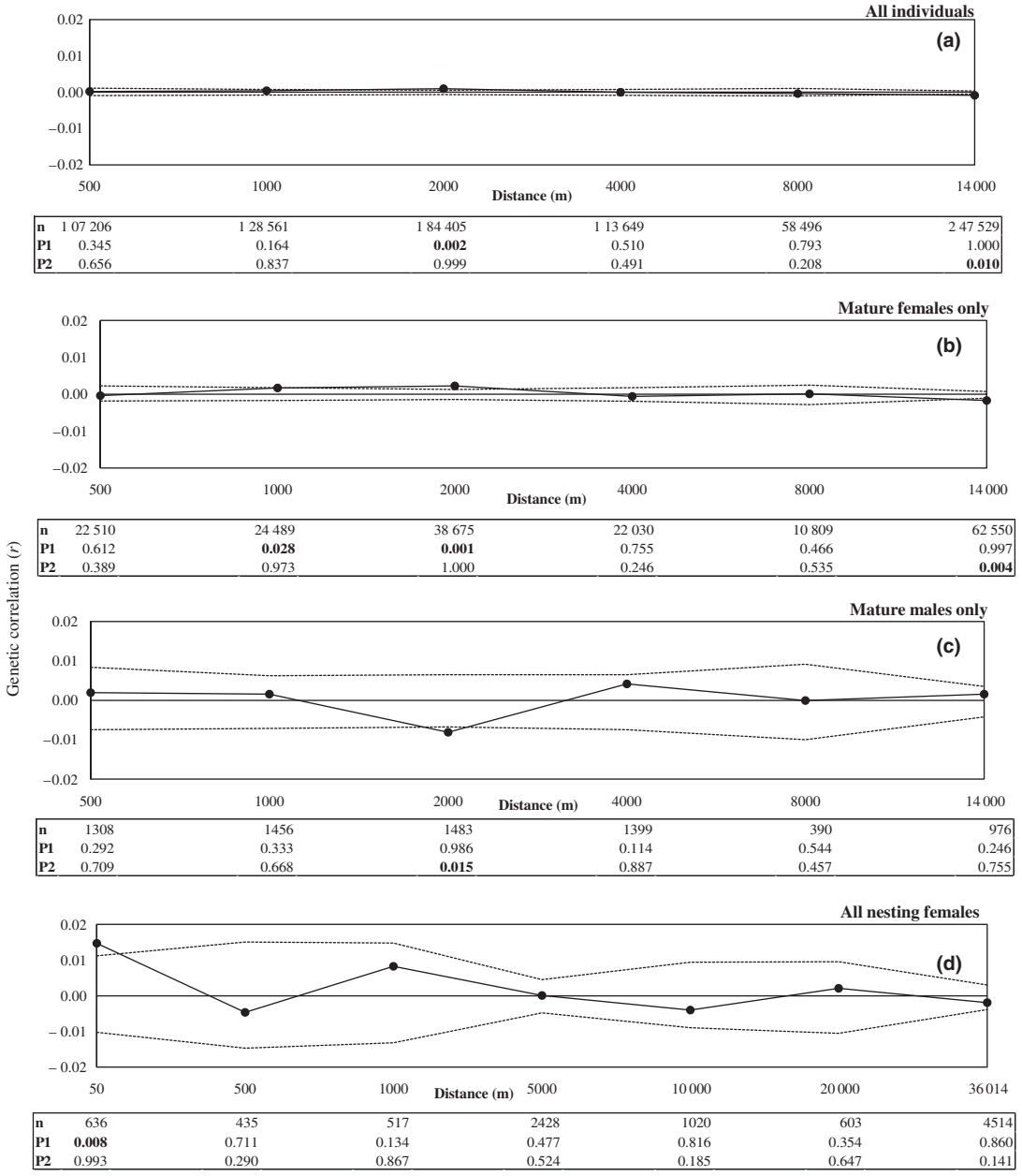

Fig. 2 Correlogram plots of the genetic correlation coefficient (r) as a function of distance for individuals genotyped and captured in North Forsythe, South Forsythe, and Island Beach State Park (a–c) and Sedge Island, Lighthouse Center, Conklin Island, West Creek, and Great Bay (d). The permuted 95% confidence interval about the null hypothesis ($r = 0$) is shown. Number of pairwise comparisons (n) for each distance class are shown. P1 is the probability that r -rand ≥ r -data and P2 is the probability that r -rand ≤ r -data, with significant values highlighted in bold.

crabbing activities and eventually lead to the extirpation of terrapins in the creek (Gibbons *et al.* 2001).

There was no significant positive genetic autocorrelation for mature males, juvenile males and juvenile females at any distance class. There was a possibility of positive spatial autocorrelation in mature females; however, the r values were very low (≤ 0.0023) and the number of pairwise comparisons (n > 20 000) increased the chance that any deviation from $r = 0$ would be significant (P. Smouse, personal communication). Thus, the pattern may not indicate any biological significance. On the other hand, in nesting females, we detected significant positive genetic autocorrelation ($r = 0.015$) from 0–50 m (maximum spatial extent 201 m) with a smaller number of pairwise comparisons ($n = 636$). The spatial autocorrelation of nesting females indicates that females

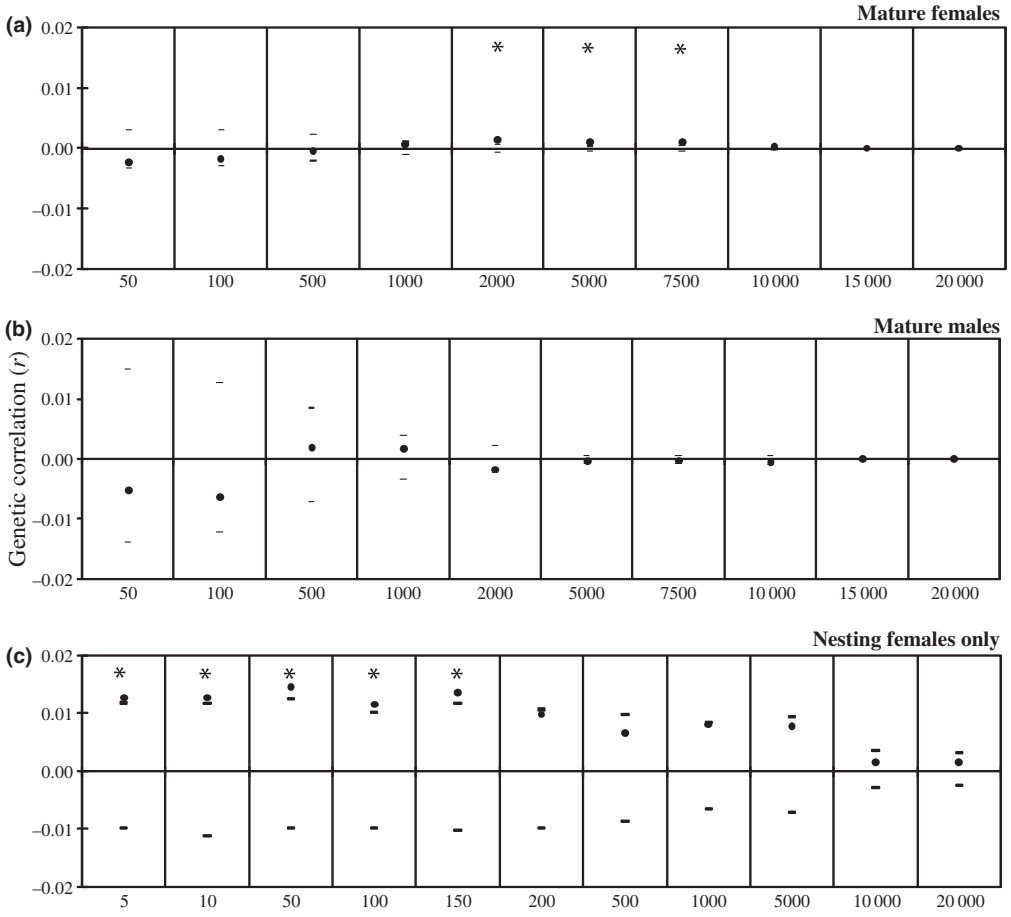

Fig. 3 Composite graphs showing the genetic correlation coefficient (*r*) from the first distance bin in each single correlogram for diamondback terrapins genotyped from North Forsythe, South Forsythe, and Island Beach State Park (a and b) and Sedge Island, Lighthouse Center, Conklin Island, West Creek, and Great Bay (c). We estimated *r* (represented by filled black circles) by successively pooling individuals into larger distance classes, i.e. 0–5 m, 0–10 m, 0–50 m, etc. Dashes bracket the 95% permuted confidence intervals about the 0 autocorrelation value, representing the null hypothesis of no spatial structure. An asterisk indicates positive spatial autocorrelation ($P < 0.05$). This graph demonstrates how the autocorrelation coefficient is affected by the size of the distance bin. Data are not shown for juvenile males and females because no positive autocorrelation values were detected for any the distance classes tested.

are exhibiting natal philopatry to nesting beaches, and the data are in agreement with a mark–recapture study that document average distances between a female's nest sites of 203 m (Szerlag & McRobert 2007).

Both our mAIc and F_0 migrant tests indicated male-biased dispersal, but F_0 migrant tests document that *per capita* there are more female than male dispersers. Because long roundtrip movements of nesting females from marsh areas to nesting areas have been documented (roundtrip 4–10 km; Butler 2002; Gibbons *et al.* 2001), it is possible that some female F_0 migrants may be foraging or mating in the area where they were captured and they may return to their natal beach to nest (i.e. a seasonal reproductive foray). Female natal homing was also recently documented in the closely related freshwater turtle species, *Graptemys kohnii* (Freedberg *et al.* 2005), where the majority of females returned to nesting locations within 160 m of their initial nesting location after translocation. Despite documentation of nest site fidelity and natal philopatry in the terrapin, we cannot exclude the possibility that some F_0 migrant females are nesting on nonnatal beaches. Indeed, three of the 33 SI nesting females included in the GENECLASS migrant tests were considered F_0 migrants. Two of the females appeared to exhibit nesting site fidelity (nesting a minimum of 2 years at the same location), while the third was only captured nesting one time.

Despite the lack natal philopatry in a handful of the females sampled, our spatial autocorrelation analysis indicates that many females are philopatric to natal beaches. Female natal philopatry might be favored by selection because it ensures that a female nests at a location that successfully hatched offspring in the previous generation, thereby increasing lifetime fitness

(Reinhold 1998; Freedberg & Wade 2001). In addition, natal philopatry in reptiles with ESD may explain why sex ratios are biased towards females (Freedberg & Wade 2001). The Freedberg & Wade's (2001) model of ESD coupled with natal philopatry demonstrates that when a nesting area is inherited maternally, a maternal lineage that produces an excess of daughters will be favored over maternal lineages producing an excess of sons.

Although the autocorrelation analysis for females on nesting beaches was significant (Fig. 2d), the relatedness among nesting females was still quite low ($r = 0.01$), considering full-siblings are expected to have a relatedness of 0.50. Several factors could play a role in slowing the accumulation of relatedness between philopatric females on a section of a nesting beach including (i) breeding group size; (ii) mean and variance in the number of successful progeny produced with each mating; (iii) the mating system; and (iv) effective movement of individuals between nesting locations (Scribner & Chesser 2001). Average coancestries (Chesser 1991) of individuals on a nesting area can be affected by the number of nesting females and the number of successful offspring produced over a female's lifetime. Given the large number of individuals captured and the low recapture rate within our study system, our nesting populations could potentially produce a large number of successful clutches from many females (sired by many males) over several years, thereby slowing the accumulation of coancestry within nesting areas. Multiple paternity within clutches can also reduce the level of relatedness within clutches to that of half-siblings ($r = 0.25$) compared to clutches with single paternity ($r = 0.50$). Multiple paternity is in common in *M. terrapin*, with 19.0–31.4% of clutches from nesting beaches in Barnegat Bay, NJ exhibiting multiple paternity (Sheridan 2010). Lastly, if some males or females effectively disperse between nesting populations, if females exhibit seasonal reproductive movement that allows them to effectively mate with males from adjacent populations or if some females do not exhibit strict natal site philopatry, then this could also lead to a reduction in the relatedness among nesting females on natal beaches.

In our study, the *m*AIc test detected the presence of sex-biased gene flow in mature males, while F_{ST}, F_{IS}, *v*AIc and average pairwise relatedness (r) did not detect any sex-biased gene flow. Mathematical simulations show that these tests differ in their sensitivity in relation to various parameters, such as dispersal rate, bias intensity, number of individuals sampled and number of loci sampled (Goudet *et al.* 2002). The F_{IS} has very low sensitivity in all cases (<70%; Goudet *et al.* 2002). The F_{ST} (and the associated average pairwise relatedness) performs best at higher dispersal rates (>10%), *v*AIc performs best at low dispersal rates (<10%) and *m*AIc is intermediate between the two tests (Goudet *et al.* 2002). It is important to note that *v*AIc and F_{ST} also performed poorly in detecting sex-biased dispersal in terrapins from Carteret County, North Carolina, but *m*AIc significantly detected male-biased dispersal (Hart 2005). Both mAIc and vAIc detected male-biased dispersal in the Florida Everglades where there was a male-biased sex ratio of 1.0:1.2 (Hart 2005). Given that the *m*AIc test detected sex-biased gene flow, we suggest that the inability of F_{ST}, F_{IS}, *v*AIc and average pairwise relatedness (r) to detect sex-biased gene flow may be attributed to several parameters (e.g. small number of loci sampled, bias intensity and population sex ratio) rather than a true lack of sex-biased gene flow.

Conservation Implications

Male-biased dispersal and female natal philopatry occurred in the diamondback terrapin. These data have important implications for both females and males. First, loss of nesting beaches could have significant negative impacts on females that attempt to return to nonexistent or altered nesting beaches. For example, females attempting to nest in an area that has been recently developed may encounter human activities, such as boat traffic, vehicles and bulkheading. If females are persistent to nest in these areas, they could suffer injury by vehicles (Wood & Herlands 1997; Hoden & Able 2003; Szerlag & McRobert 2006) and motorboats (Gibbons *et al.* 2001; Tucker *et al.* 2001; H. W. Avery, unpublished), or nest failure. Female terrapins continue return to nest in Margate, NJ, a barrier island with most of its bay front lined with bulkheading and are usually unsuccessful (R. Scott, personal communication).

Second, if females cannot find alternative nest locations, then dystocia (egg-binding) may occur. The lack of suitable habitat for nesting can cause female turtles to retain eggs in the oviducts, both in captivity (Miller 1932; Risley 1933; Cagle & Tihen 1948; Jackson *et al.* 1971) and under natural conditions (Galbraith *et al.* 1988; Buhlmann *et al.* 1995). In some cases, egg retention leads to the movement of eggs into the abdominal cavity (Risley 1933; Cagle & Tihen 1948; Jackson *et al.* 1971). Eggs in the abdominal cavity can become infected with bacteria, cause inflammatory reactions (Jackson *et al.* 1971) and could lead to death.

Third, females remaining philopatric to degraded nesting beaches could lay nests with reduced hatching success. Overall, the alteration or loss of nesting beaches could lead to a reduction in the reproductive

success, changes in population sex ratios and long-term viability of terrapin populations.

Fourth, as males are more prone to disperse than females, it is important to reduce threats to males particularly during dispersal. Threats to males include boat mortality (Tucker *et al.* 2001; Cecala *et al.* 2008), road mortality (Hoden & Able 2003), crab pot mortality (Bishop 1983; Roosenburg *et al.* 1997; Dorcas *et al.* 2007), pollution (Burger 2002; Basile, unpublished) and predation (Cecala *et al.* 2008). Maintaining gene flow via males, especially in populations with male-bias sex ratios (e.g. Kiawah Island, South Carolina, 1:1.78 male biased; Lovich & Gibbons 1990), will be particularly important for the conservation of this species. Although females are less prone to disperse between populations, the strong female-biased ratio (mature individuals only *c.* 5:1; all individuals *c.* 1.64:1) in our population indicates that gene flow may be primarily mediated by females. Gene flow could occur during the seasonal reproductive movements of female terrapins. Thus, females should be protected from anthropogenic impacts, particularly in populations with female-bias sex ratios.

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This research was conducted as part of C.M.S.'s doctoral research. C.M.S. is broadly interested in using molecular genetic tools in aiding management guidelines for the conservation of species. J.R.S.'s research interests are centred in the areas of environmental science, physiological and biophysical ecology, fisheries biology and ichthyology, as well as conservation biology. W.F.B.'s research focuses primarily on natural resource management, restoration ecology, conservation biology, and Pinelands community dynamics. H.W.A.'s research interests in ecology are broadly based on how variations of environmental resources are transduced through individuals into population dynamics of wild animal populations.
