

1 **Title.**—Nesting success and barrier breaching: Assessing the effectiveness of roadway
2 fencing in Diamondback Terrapins (*Malaclemys terrapin*)

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27 **Abstract.**—Roads can adversely affect animal populations by impacting nesting behavior,
28 causing roadway mortality, and fragmenting or reducing habitat. Fences have frequently
29 been implemented to combat direct road mortality, but at the expense of changing
30 patterns of nesting behavior and increasing population fragmentation. I studied the
31 effectiveness of barrier fences that were installed to reduce road mortality in nest-seeking
32 diamondback terrapins (*Malaclemys terrapin*) along two causeways in coastal southern
33 New Jersey. To determine whether the barriers limited roadway access, I surveyed the
34 ground adjacent to the fences for evidence of terrapin nest holes in relation to the barrier,
35 indicating whether terrapin nesting activity occurred on the marsh side of the fence or on
36 the road side. As a second direct measure of effectiveness, I created a corrugated tubing
37 arena and documented terrapin escape success to examine barrier breaching. Fences
38 were generally effective in restricting terrapin movement: I found far fewer road-side
39 nests than marsh-side nests, as well as a spatial clustering of road-side nests near the free
40 ends of the fence at one field site. Additionally, the barrier breaching success was
41 positively correlated with gap size between the fence and the ground, irrespective of
42 terrapin body size, indicating that diligent fence maintenance is imperative. Given
43 terrapins' high probability of road mortality, sensitive life history traits, and widespread
44 population declines, I conclude that fences are currently essential in their conservation
45 and may warrant greater consideration in the field of turtle conservation, particularly in
46 species with nesting movements that intersect with roads.

47

48 **Key Words.**—barrier fence; habitat fragmentation; gravid females; nesting success; road
49 mortality; turtle; wetlands conservation

50

INTRODUCTION

51 With land development and road networks constantly expanding in the United
52 States, road construction has likely contributed to significant population declines in
53 mammals, birds, amphibians, and reptiles (Ashley and Robinson 1996; Gibbs and Shriver
54 2002). Roads affect populations by impacting nesting behavior, fragmenting habitat, and
55 causing direct road mortality (Dodd et al. 2004). Once limited by topography, roads can
56 now expand into previously undeveloped habitats and threaten an ever-increasing number
57 of species (Ashley and Robinson 1996).

58 For the last few decades, biologists and engineers have tested and developed a
59 number of potential solutions to the problem of roadway access by dispersing or nesting
60 animals, which often leads to direct road mortality (Dodd et al. 2004). A common
61 mitigation strategy is the installation of temporary fence-culvert systems to prevent
62 roadway access and facilitate dispersal (Aresco 2005; Dodd et al. 2004). Aresco (2005)
63 installed this type of system on a section of a highway crossing Lake Jackson, Florida,
64 and reported that mortality of turtles and other herpetofauna declined significantly after
65 installation. Dodd et al. (2004) assessed the effectiveness of a barrier wall-culvert system
66 built on a section of highway in Alachua County, Florida and found that snake, turtle, and
67 alligator mortality decreased dramatically post-construction. To alleviate impacts of a
68 highway constructed through the center of one of the largest French populations of
69 Hermann's tortoise (*Testudo harmanni*), Guyot and Clobert (1997) relocated 300
70 tortoises directly affected by the construction and installed fences and a culvert-tunnel
71 system under the road to provide for safe movement of animals across the road. Road

72 mortality was low in the four years following highway construction, and a mark-
73 recapture study indicated that the adult population was stable (Guyot and Clobert 1997).

74 In the United States, turtles may be especially impacted by roads as compared
75 with other animals. The United States has high turtle diversity (Ernst and Barbour 1989),
76 but all tortoises and about one third of aquatic and semiaquatic turtles currently require
77 conservation action (Lovich 1995; Gibbs and Shriver 2002). Roads are expected to have
78 contributed to turtle population declines because turtles have sensitive life history traits
79 including high adult survival rates and delayed sexual maturity (Wilbur and Morin 1988;
80 Gibbs and Shriver 2002). Turtle populations are therefore constrained in their ability to
81 deal with additive annual mortality due to anthropogenic impacts (Gibbs and Shriver
82 2002), and studies indicate that only 2-3% additive annual mortality is more than most
83 turtle species can cope with to maintain population stability (Congdon et al. 1993, 1994;
84 Gibbs and Shriver 2002).

85 Barrier effectiveness is often defined by the extent to which barriers reduce road
86 mortality or prevent animals from accessing the road (Dodd et al. 2004; Aresco 2005).
87 The most direct measure of barrier effectiveness is documenting roadkills. However,
88 roadkills are highly ephemeral and difficult to measure accurately as predators,
89 scavengers, and cars can remove this form of evidence within hours, especially for small
90 animals. In species that encounter roads when searching for nesting habitat, an
91 alternative, longer-lasting metric of barrier efficacy involves measuring nesting
92 characteristics in relation to the fence. When the land on both sides of the barrier is
93 equivalent in terms of area, moisture, substrate, and vegetation, the location of the nest

94 (i.e. habitat-side of the barrier or road-side of the barrier) is an important metric to assess
95 barrier effectiveness, as the distribution should be equal if the fence is ineffective.

96 For turtles, the disposition of the observed nests (i.e. whether the nest has been
97 predated, or attempted before abandonment) is another useful metric of barrier
98 effectiveness. For many turtles including diamondback terrapins (*Malaclemys terrapin*),
99 successfully laid nests are often difficult to detect due to their cryptic concealment, but
100 high rates of nest predation within 48 hours of oviposition (as observed in various turtle
101 species) make predated nests a useful indicator of nesting activity. Butler et al. (2004)
102 monitored daily nesting by diamondback terrapins for two summers and found 81.9% (in
103 1997) and 86.5% (in 2000) of nests were predated, and Feinberg and Burke (2003)
104 similarly recorded diamondback terrapin nest predation of 92.2%. Therefore, predated
105 nests are a good measure of egg-laying activity and make a reasonable proxy for
106 successful nests resulting in hatchlings. While predated nests represent a high percentage
107 of successfully laid nests, nest abandonment before egg-laying can be as common as
108 completing a nest (Roosenburg 1994), so additional documentation of abandoned nests
109 gives a more complete picture of female movement during this critical nesting phase.

110 Further, directly observing animals' barrier breaching success when faced with a fence is
111 another useful metric to assess barrier effectiveness, providing better understanding of the
112 conditions under which fences are likely to be breached by females of different body
113 sizes. This pairing of nest observations with behavioral tests can thus provide robust,
114 inclusive estimates of general fence effectiveness for adult females, which is especially
115 important in species with sensitive life history traits like turtles.

116 Among all species of turtles, diamondback terrapins may be exceptionally
117 vulnerable to anthropogenic impacts. Diamondback terrapins are a species of emydid
118 turtle whose populations have declined range-wide due to various human activities, one
119 of which is road construction (Seigel and Gibbons 1995; Dorcas et al. 2007; Grosse et al.
120 2011). Terrapins have been disproportionately impacted by habitat development and
121 roadway construction, mainly due to their sensitive life history traits (i.e., delayed sexual
122 maturity, low reproductive rates, long lifespans, and high home site fidelity) and unique
123 habitat requirements (Gibbons et al. 2001; Seigel and Gibbons 1995). The species' range
124 is several thousands of miles long but only a few miles wide, extending along the Atlantic
125 Coast from Massachusetts to southernmost Florida and around the Gulf Coast to Texas
126 (Ernst et al. 1994; Wood and Herlands 1997). Terrapins are the only turtle species in the
127 world exclusively adapted to brackish water coastal salt marshes (Ernst et al. 1994; Wood
128 and Herlands 1997). Coastal salt marshes in the United States have been heavily
129 impacted by industrial and real estate development over the past century, thus destroying
130 a great deal of terrapin habitat and reducing access to nesting sites (Wood and Herlands
131 1997).

132 Along the Atlantic coast of New Jersey, terrapins' natural nesting habitat (sand
133 dunes on barrier beach islands) has largely disappeared due to human encroachment.
134 Large numbers of terrapins now nest on the shoulders of heavily trafficked roads adjacent
135 to salt marshes (Wood 1997), as terrapins must lay their eggs above the high tide line
136 (Roosenburg and Place 1994; Butler et al. 2004). Nesting alongside heavily trafficked
137 roads results in substantial roadway access and mortality within some parts of their range.
138 Terrapins' sensitive life history traits and unique habitat requirements lead to roads

139 disproportionately affecting the species, thus making them an ideal model system for
140 installing barrier fences to reduce roadway access and assessing barrier effectiveness.

141 Terrapins' vital role in salt marsh biodiversity maintenance further qualifies them
142 as an ideal system to test the effectiveness of barriers. Coastal salt marshes are one of the
143 most dynamic, diverse, and productive natural systems on earth (Ashley and Robinson
144 1996). Terrapins play an essential role in the maintenance of salt marsh biodiversity by
145 controlling the density of the marsh-grazing periwinkle (*Littoraria irrorata*) (Silliman
146 and Bertness 2002). Silliman and Bertness (2002) experimentally demonstrated that the
147 high plant production in eastern coastal salt marshes is ultimately realized through a
148 trophic cascade, where marine predators such as terrapins limit the densities of plant-
149 grazing snails that are capable of devastating marshes. This suggests that significant
150 declines in terrapin populations could alter the structure and function of salt marsh
151 habitats (Silliman and Bertness 2002).

152 Although anthropogenic impacts contributing to terrapin declines include
153 commercial harvest for food (Wood and Herlands 1997; Gibbons et al. 2001), incidental
154 drowning in crab traps (Wood and Herlands 1997; Gibbons et al. 2001; Dorcas et al.
155 2001), road mortality (Seigel and Gibbons 1995; Wood and Herlands 1997), habitat
156 destruction and fragmentation (Wood and Herlands 1997), and accidental capture in
157 storm drains (Grottola et al. 2010), road mortality is the most obvious and one of the most
158 important contributors to terrapin mortality along the Atlantic coast of southern New
159 Jersey. Well over 10,000 terrapin roadkills were documented between 1989 and 2011 in
160 Cape May County, New Jersey (McLaughlin 2011). Since 2004, both scientists and
161 community volunteers have attempted to combat this source of terrapin mortality by

162 developing and installing various types of terrapin barrier fences designed to restrict nest-
163 seeking females to the marsh-side of the barrier. The barrier fence installation techniques
164 and materials have been refined over the years, first using silt, then plastic mesh, and now
165 plastic corrugated tubing. Corrugated tubing is currently favored because it is relatively
166 less conspicuous, easy to install, and more durable than previous fence materials. Over
167 12,000 feet of barrier fences have been installed along the coast of southern New Jersey
168 (McLaughlin 2011).

169 Anecdotally, the barrier fences appear effective in reducing terrapin roadway
170 access, but there had been no assessment until this study. The primary objective of my
171 study was to assess terrapin barrier effectiveness as a means to reduce nest-seeking
172 terrapins' access to the roads. To determine barrier effectiveness, I first surveyed the
173 ground adjacent to the fences for evidence of terrapin nest holes in relation to the barrier,
174 indicating whether terrapin nesting activity occurred on the marsh side of the fence or on
175 the road side. As a second measure of effectiveness, I created a corrugated tubing arena
176 and documented terrapin escape success to determine the likelihood of barrier breaching.
177 Determining barrier effectiveness is critical to understanding how barriers impact adult
178 female nesting behavior, ensuring that conservation efforts and resources are being
179 properly allocated, and identifying opportunities for improvement in barrier design to
180 protect the species better in those parts of its range where roadkills during nesting season
181 are a significant problem.

182

183

MATERIALS AND METHODS

184 **Study Species.**—Diamondback terrapins (*Malaclemys terrapin*) are estuarine,
185 emydid turtles whose range extends from the northern tip of Cape Cod, Massachusetts to
186 the Gulf Coast of the United States (Ernst et al. 1994; Wood and Herlands 1997). Within
187 this range are seven subspecies (Wood and Herlands 1997). I focused my study on a
188 population of the northernmost subspecies, the northern diamondback terrapin
189 (*Malaclemys terrapin terrapin*), which is found from Massachusetts to North Carolina
190 (Wood and Herlands 1997).

191 Terrapins nest for approximately six weeks from mid- late-May to mid- late-July
192 (Goodwin 1994; Wood 1997; Butler et al. 2004). Many hatchlings emerge after a 10-11
193 week incubation period (Roosenburg 1991; Goodwin 1994; Butler et al. 2004), but in
194 northern parts of their range including my study area, some remain in their nests
195 throughout the winter and emerge the following spring (Wood 1997).

196

197 **Study Site.**—I studied two sections of roadway that connect the mainland to
198 coastal barrier islands on the Atlantic Coast of southern New Jersey. Stone Harbor
199 Boulevard (SHB), Cape May County (39.06°N, 74.77°W) and the Margate Causeway
200 (MC), Atlantic County (39.34 °N, 74.54 °W) were chosen as representative of the many
201 causeways in the area that cross salt marshes and have terrapins nesting on their
202 embankments. I surveyed a 589 m section of the SHB and a 623 m section of the MC
203 (Fig. 1). Both causeways cross salt marshes dominated mainly by saltmarsh cordgrass
204 (*Spartina alterniflora*) and saltmeadow cordgrass (*Spartina patens*). Salinity is generally
205 30-32 ppt, similar to that of the nearby ocean, and tidal amplitude within the marsh is
206 about 1.5 m (Wood and Herlands 1997).

207 Embankments alongside the causeways range in width from less than 1 m to 10 m
208 in parts of the MC. The upper slopes of these embankments create a suitable nesting
209 habitat for terrapins seeking high ground. Crabgrass and other vegetation cover the sandy
210 embankments. These salt marshes are no longer subject to development, but the
211 waterways and causeways passing through and across them are used heavily by humans,
212 particularly in the summer months (Wood and Herlands 1997). There has been
213 considerable alteration of both the mainland and barrier beach island sides of the
214 marshes, so while some of the salt marsh has been preserved, natural terrapin nesting
215 sites on sand dunes above the high tide line have largely been destroyed (Wood and
216 Herlands 1997) or rendered inaccessible by bulkheading. This development has forced
217 terrapins to seek alternative nesting habitat along the embankments of the causeways that
218 cross salt marshes.

219

220 ***Field Survey: Nest Census.***—I surveyed the north and south sides of the two
221 roads, both previously fenced with six inch diameter corrugated tubing staked in place at
222 ground level, for evidence of terrapin nesting activity. Fences were installed on the
223 embankments such that the microhabitat characteristics and the total area of searchable
224 nesting habitat on both sides were approximately equal. There was no noticeable
225 difference in plant assemblage or moisture gradient. Preliminary data comparing fenced
226 and unfenced roadways suggest that the distribution of nests across the strip of land
227 between the road and the marsh is uniform (data not shown). During 2011, I surveyed
228 both sides of each road once a week from 17 June through 8 July. Based on the results
229 from 2011, I refined my methods and sampled less frequently, but more intensively, in

230 2012 by surveying both sides of each road twice between 7 June and 4 July. During
231 every survey, I documented terrapin nest holes by walking along the marsh side of the
232 fence in one direction and on the road side in the other direction to ensure that all nest
233 holes were recorded. I randomly selected which end of the fence to begin each survey
234 on. I completed all surveys to control for observer bias.

235 For each nest hole, I recorded the road name, whether it was on the north or south
236 side of the road, whether it was on the marsh side or road side of the corrugated tubing
237 barrier, GPS location (using a Magellan Triton), and the distance (in meters, to the
238 nearest centimeter) from the corrugated tubing. I used a 10 m rolling tape measure to
239 record the straight-line minimum distance (to the nearest centimeter), and I flattened
240 vegetation that was in the way to measure more accurately.

241

242 **Field Survey: Predation.**—Predated and abandoned nests reflect nesting activity
243 as they indicate where terrapins attempted to nest. Both predated (Fig. 2a) and
244 abandoned (Fig. 2b) nests appear as shallow, circular excavations approximately 4-6 cm
245 in diameter and 10-15 cm in depth. Abandoned nests may be smaller if they were not
246 completed before abandonment. Terrapin nest holes are distinguishable from other
247 depressions in the ground as they curve to the side at the base of the hole, forming a ‘J’
248 shape. Nests predated by common mammalian predators (e.g. raccoons, *Procyon lotor*;
249 skunks, *Mephitis mephitis*; red foxes, *Vulpes vulpes*) were identified by eggshells
250 scattered nearby. I estimated the number of eggs per predated nest by piecing together
251 the eggshells, which were often broken into halves or thirds of the original whole eggs.
252 However, some predators (e.g., fish crows, *Corvus ossifragus*) eat eggs whole and leave

253 little or no evidence of their predation. There is no definitive way to recognize this type
254 of predation, so holes without eggshells were counted as abandoned nests. To prevent
255 double counting of nests, I filled in each hole after recording it and collected all predated
256 eggshells. Nests do not remain visible for more than one season, as rain and flooding fill
257 in the holes and wash away old eggshells.

258

259 *Arena Experiment.*—Terrapins can occasionally reach the road side of the
260 barriers by crawling underneath the corrugated tubing in areas where gaps have formed.
261 Gaps may be formed where corrugated tubing spans ground depressions, or they may
262 result from vegetation growing upwards underneath the corrugated tubing. To
263 understand how such gaps influence barrier effectiveness, I built a five m oval arena of
264 corrugated tubing and raised a section of the tubing to various heights (0-8 cm). I placed
265 adult female terrapins (N = 40 individuals; 74 trials) individually in the arena and
266 observed the number of terrapins that escaped through the gap within 10 min. I measured
267 the height of the terrapins and recorded gravidity. Gravidity was assessed by holding the
268 terrapin on her side, placing fingers in the area just in front of her hind limbs, and
269 palpating the oviducts for shelled eggs. I tested only adult females, as males typically
270 never emerge from the safety of the salt marsh. This experiment was run for three
271 consecutive summers during June and July. In 2010 and 2011, the arena was placed on a
272 flat area of grass and a range of gap sizes (0, 2.5, 3.8, 6.4, and 7.6 cm) was tested. Based
273 on these results, I also tested gaps of 5.1 cm in 2012 to compliment the sizes evaluated in
274 previous years. I tested each individual for one or two gap sizes, so gap size and location
275 within the arena were randomly selected each trial. I considered each trial to be

276 independent. Terrapins typically crawled straight to the barrier, unsuccessfully attempted
277 to climb over the tubing, and then proceeded to walk along the inner circumference of the
278 tubing, occasionally attempting to crawl over or under it.

279

280 **Data Analysis.**—All of the nest locations were plotted on Google earth images
281 using R package ‘Google Maps’ (R version 2.15.2). I combined the two years of field
282 survey data (N=560) and three years of arena experiment data (N=40 individuals; 74
283 trials) for analysis. The field survey results, specifically whether the nest holes were on
284 the marsh side or the road side of the fence, were tested for normality and homogeneity
285 of variance using SAS 9.3 (SAS Institute 2011). I evaluated the effect of marsh vs. road
286 side of fence, north vs. south side of causeway, and site, as well as the interactions among
287 these variables, on the number of predated and abandoned nests using chi-square analysis
288 in R for each comparison. I calculated the average road length by summing the distances
289 on both sides of the road and dividing by two, and they are essentially identical for both
290 study sites: (MC: $(540.6 + 623.3)/2 = 581.9$ m; SHB: $(575.3 + 589.2)/2 = 582.2$ m).
291 Thus, I used raw nest counts for subsequent analyses instead of adjusting these values per
292 km.

293 Furthermore, to assess barrier efficacy and test whether nests on the road side of
294 the fence were closer to the free ends of the fenced sections than marsh-side nests, I used
295 Monte Carlo resampling in R to compare the observed and expected distributions of road-
296 side nest distances. I converted each nest coordinate from decimal degrees to UTM using
297 a batch conversion worksheet in MS Excel (available at: uwgb.edu, date accessed: 27
298 September 2013). For each site independently, I used the UTM coordinate of each nest

299 to calculate the shortest straight-line distance in meters between each nest and its nearest
300 fence-end to generate an observed distribution of distances for the road side of the fence.
301 To create a test statistic representing this distribution, I calculated the median distance
302 within this observed distribution. I then resampled (100,000 repetitions) the full
303 distribution of distances for each site to generate expected distributions of road-side
304 distances with the same number of nests as the observed road-side distributions (N = 14
305 for SHB, N = 20 for MC) and similarly calculated the median for each simulated
306 distribution.

307 I analyzed the arena experiment by logistic regression of proportional success vs.
308 gap size and terrapin height. All statistical tests were performed using R, and I assessed
309 significance at $P < 0.05$.

310

311

RESULTS

312 ***Field Survey: Nest Census.***—I first assessed whether there was variation among
313 sites and years to ensure that terrapin nesting behavior was similar across these variables.
314 I found a significantly greater number of nests on Stone Harbor Boulevard than on the
315 Margate Causeway ($\chi^2 = 146.06$, $df = 1$, $P < 0.001$). In terms of year, there was a
316 weaker, yet significant effect, with slightly more nests found in 2012 than 2011 ($\chi^2 =$
317 4.829 , $df = 1$, $P = 0.028$). I found no interaction between year and site ($\chi^2 = 5.032$, $df =$
318 1 , $P = 0.249$). Because site effect is more biologically relevant and has a stronger
319 statistical effect, I only consider site differences in the subsequent analyses.

320 Orientation (north vs. south side of road) played no role in nesting activity ($\chi^2 =$
321 0.714 , $df = 1$, $P = 0.398$) when considering all data. The interaction between site and

322 orientation was not significant ($\chi^2 = 1.193$, $df = 1$, $P = 0.275$). When analyzing within
323 site, orientation did not impact nesting activity on either road (MC: $\chi^2 = 2.110$, $df = 1$, P
324 $= 0.146$; SHB: $\chi^2 = 0.021$, $df = 1$, $P = 0.884$).

325 When considering all data, I found a significantly greater number of nests on the
326 marsh side of the corrugated tubing barriers than on the road side ($\chi^2 = 414.86$, $df = 1$, P
327 < 0.001). When analyzing within site, both roads had significantly more nests on the
328 marsh side of the barriers than on the road side (MC: $\chi^2 = 68.679$, $df = 1$, $P < 0.001$;
329 SHB: $\chi^2 = 350.414$, $df = 1$, $P < 0.001$). (Fig. 3). I separated the dataset by site in order to
330 look at the effect on each road. Chi-square analysis of both site and fence side revealed a
331 significantly greater number of road-side nests on the MC than on the SHB ($\chi^2 = 14.792$,
332 $df = 1$, $P < 0.001$).

333 I found that on the SHB, road-side nests were closer to the fence-ends than
334 expected by chance ($P < 0.001$), but I found no such spatial effect on the MC ($P = 0.131$;
335 Fig. 4).

336

337 **Field Survey: Predation.**—There was a site effect on predation such that nests on
338 the SHB were more often predated than those on the MC ($\chi^2 = 15.085$, $df = 1$, $P < 0.001$).
339 Within-site analyses revealed that there was more abandonment than predation on the
340 MC ($\chi^2 = 12.270$, $df = 1$, $P < 0.001$; Fig. 5a) but marginally more predation than
341 abandonment on the SHB ($\chi^2 = 3.596$, $df = 1$, $P = 0.058$; Fig. 5b).

342 I found a year effect on predation, such that predation was more common in 2011
343 than in 2012 ($\chi^2 = 9.2897$, $df = 1$, $P = 0.002$). I found an interaction between year and
344 predation such that globally, predation was higher in 2011 than 2012 ($\chi^2 = 9.290$, $df = 1$,

345 $P = 0.002$). However, within-site analyses showed evidence of an interaction effect with
346 trends in opposite directions; the effect was significant on the MC ($\chi^2 = 14.433$, $df = 1$, P
347 < 0.001) but only marginally significant on the SHB ($\chi^2 = 3.304$, $df = 1$, $P = 0.069$).

348 When all data were considered simultaneously, I found that predation and fence-
349 side (marsh vs. road) were not related ($\chi^2 = 1.0389$, $df = 1$, $P = 0.308$). Similarly, neither
350 within-site analysis showed an interaction between predation and fence side (MC: $\chi^2 =$
351 0.573 , $df = 1$, $P = 0.449$; SHB: $\chi^2 = 2.170$, $df = 1$, $P = 0.141$).

352

353 ***Arena Experiment.***—I fit a logistic regression to the data and found that
354 increasing gap size below the fence was correlated with increasing escape success ($Z =$
355 4.373 , $df = 73$, $P < 0.001$) (Fig. 6). I found that gravidity of the terrapin did not impact
356 escape success ($Z = 1.227$, $df = 73$, $P = 0.220$). Carapace length, used as an estimate of
357 size, was not correlated with escape success ($Z = 0.623$, $df = 56$, $P = 0.533$).

358

359

DISCUSSION

360 I found that the fences were effective in reducing terrapins' road access, but
361 efficacy depended on microenvironmental factors, and was not constant within or
362 between sites. These results have important implications for understanding the ecological
363 tradeoffs associated with fences and recommendations for the management of terrapins
364 and other wetlands species.

365 Barrier fences were highly effective in restricting nest-seeking terrapins to the
366 marsh side of the barriers, and therefore substantially decreased roadway access, and its
367 subsequent mortality, in my study sites. Given that terrapins emerge from the marsh, it is

368 evident that the fences had an effect on roadway access and available nesting habitat; if
369 the fences had no effect, one would expect to find equal numbers of nests on both sides of
370 the barrier. Fences have been reported to work especially well in reducing mortality of
371 turtles as compared with various animal groups (Boarman and Sazaki 1996; Barichivich
372 and Dodd 2002; Dodd et al. 2004; Aresco 2005). However, fence usage is often
373 controversial because there are ecological tradeoffs associated with fences, as they may
374 create barriers to dispersal, migration, and gene flow (Jaeger and Fahrig 2004; Aresco
375 2005; Hayward and Kerley 2009). Fragmentation may be especially detrimental to
376 terrapin populations due to their high site fidelity (Gibbons et al. 2001). Barriers to
377 dispersal could further limit gene flow in species that already have restricted migration.
378 Furthermore, it is important to consider the effects of fragmentation and roadway
379 mortality on terrapins, despite only nest-seeking females being affected, as both
380 anthropogenic impacts could have significant population-wide consequences; population
381 model analyses for loggerhead sea turtles indicate that an annual loss of only a few
382 hundred subadult and adult female turtles can have a profound impact on population
383 dynamics (Heppell et al. 1996).

384 Jaeger and Fahrig (2004) used a simulation model to determine whether fences
385 enhance or reduce the effect of roads on population persistence in various species, and
386 they reported that the impact of the fence depends on an animal's degree of roadway
387 avoidance and its probability of roadway mortality upon entering the road. For species
388 with high traffic mortality rates, fences generally enhance population persistence,
389 especially when populations faced additional sources of anthropogenically-induced
390 mortality. In my study area and throughout their range, terrapins qualify as a species

391 with a high likelihood of roadway mortality, low road avoidance, and multiple sources of
392 mortality. Therefore, the model indicates that fences would likely enhance population
393 persistence of terrapins despite the fragmentation tradeoff. In combination with my
394 finding that fences are highly effective in restricting nest-seeking terrapin movement, I
395 conclude that fences are currently necessary in maintaining terrapin populations in
396 southern New Jersey.

397 Turtles may be particularly susceptible to road mortality because their life
398 histories are characterized by high adult survivorship, delayed sexual maturity, and low
399 annual recruitment (Congdon et al. 1993), and many species' life cycles incorporate
400 terrestrial movements that often intersect with roads (Gibbons 1986). When this occurs,
401 turtles are especially vulnerable to roadway mortality due to low road avoidance and low
402 travel speed (Steen and Gibbs 2004), so barrier fencing could be a highly effective
403 management strategy for many turtle species beyond terrapins, despite the barrier-
404 induced fragmentation effects. Turtle life history traits limit populations' ability to
405 absorb the loss of sexually mature adults (Brooks et al. 1991), so fences that restrict the
406 movement of nesting or dispersing individuals may warrant greater consideration in the
407 field of turtle conservation.

408 My results also indicate that fence effects and ecological tradeoffs are dependent
409 upon site differences and local conditions. Across sites, the fences were effective in
410 reducing overall road access, but barrier breaching varied within and between sites and
411 depended on microenvironmental factors including elevation, flooding, and vegetation.
412 Barrier breaching was more common on the MC, as road-side nests represented a greater
413 proportion of total nests as compared with the SHB nests. MC had lower elevation (4 m)

414 than SHB (6 m), greater flooding, and excess vegetation growth along its embankments
415 (pers. obs.). Vegetation can create gaps beneath the fence and provide terrapins with a
416 bridge over the fence. Further, MC fences were newer than SHB fences, and it has been
417 observed that corrugated tubing barrier effectiveness increases with time, barring
418 damage, as the fences sink into the ground and kill the vegetation underneath. New
419 fences are light and sit on top of live vegetation, making it much easier for terrapins to
420 crawl beneath (pers. obs.). Fence effectiveness and subsequent ecological tradeoffs
421 depended heavily on local conditions, so management plans and maintenance should be
422 carefully tailored to complement microenvironmental conditions.

423 These findings were supported by my arena experiment results, which
424 demonstrated that barrier breaching success was positively correlated with gap size
425 between the bottom of the fence and the ground surface, irrespective of terrapin body
426 size. Interestingly, gravidity of the terrapins did not impact escape success, so females
427 before and after oviposition were equally likely to breach the barriers. This unexpected
428 result is encouraging, indicating that efforts to target adult females for protection are not
429 being hindered by gravid female determination to overcome the barriers. Examining
430 female body size and gravidity in relation to barrier behavior was a novel approach.

431 Similarly, predation and spatial placement of nests in relation to the barrier
432 depended on local conditions. Because there was a spatial clustering of road-side nests
433 near the free-end of one SHB fence, this suggests that the SHB fence was even more
434 effective than the road-side nest counts indicated, as terrapins likely accessed this area by
435 walking around the fence-end or emerging from the marsh in an unfenced section and
436 walking to the fenced zone. This pattern was not found on MC, as road-side nests were

437 more evenly scattered throughout the fence. The MC study site was a small island, so
438 accessing the road from beyond fenced sections was not possible. Predation patterns also
439 varied between sites, likely caused by microenvironmental differences in elevation,
440 flooding, and vegetation. Further, fence side and predation were not related, so fences
441 did not seem to be offering protection from predation or altering predator behavior.
442 Fence-related effects seem to depend on local conditions, so it may not be possible to
443 draw certain generalizations across sites.

444 Based on the results of my study, I offer a few basic recommendations for the
445 conservation of terrapins (or other marshland specialists) subject to road mortality. This
446 study demonstrates that significant decreases in roadway access can be achieved through
447 simple, low-cost management practices. Corrugated tubing fences have a measurable
448 impact and are relatively easy, inexpensive, and fast to install. In order to optimize fence
449 effectiveness, maintenance of the fence, vegetation, and ground is imperative during
450 nesting season. This can be accomplished via vegetation management, filling gaps
451 beneath fences with sediment, and regularly replacing broken fence stakes. New
452 approaches should be investigated, including strategies to modify the fence-ends to
453 prevent the spatial clustering of road-side nests near fence-ends, as seen on the SHB.
454 Fences should always curve outward toward the marsh at their ends and extend all the
455 way to the water, if possible. Further studies are needed to develop new techniques for
456 weighing down the fences and more permanently attaching fences to the ground.

457 Given the limited funding available in conservation management, efficient use of
458 resources is critical (James et al. 1999). Management of wetlands species, specifically
459 dual-environment species, can be difficult, and conservation plans must be designed

460 within the context of how the species uses its multiple habitats (Pressey 1994; Law and
461 Dickman 1997). If regional populations are to persist, management plans must
462 accommodate the nesting migration and local movements of turtles and other species
463 (Gibbs and Amato 2000; Gibbs and Shriver 2002). By focusing my study on terrestrial
464 nesting activity, I show that fences can effectively address the problem of female-biased
465 roadway access, and subsequent mortality, in this dual-habitat species. Protecting adult
466 females in species with sensitive life history traits can have significant population-wide
467 consequences (Wilbur and Morin 1988), so fences that reduce mortality of adult females
468 represent an efficient use of conservation resources. My results are encouraging and may
469 be useful in situations dealing with complex habitat usage, as often is found in wetlands
470 systems. Multiple habitat usage can complicate conservation efforts, but targeted
471 protection of adult females could significantly help long-lived species cope with additive
472 mortality.

473

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498

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LITERATURE CITED

500 Arseco, M.J. 2005. Highway mortality of turtles and other herpetofauna at Lake Jackson,
501 Florida, USA, and the efficacy of a temporary fence/culvert system to reduce
502 roadkills. Pp 433–449 *In* Proceedings of the International Conference on Ecology
503 and Transportation. C.L. Irwin, P. Garrett, and K.P. McDermott (Eds.). Center for
504 Transportation and the Environment, North Carolina State University, Raleigh,
505 NC.

506

507 Ashley, E.P., and J.T. Robinson. 1996. Road mortality of amphibians, reptiles and other
508 wildlife on the Long Point Causeway, Lake Erie, Ontario. Canadian Field
509 Naturalist 110:403–412.

510

511 Barichivich, W.J., and C.K. Dodd Jr. The effectiveness of wildlife barriers and
512 underpasses on US Highway 441 across Paynes Prairie State Preserve, Alachua
513 County, Florida. Phase II Post-Construction Final Report. No. Final Report. 2002.

514

515 Boarman, W.I., and M. Sazaki. 1996. Highway mortality in desert tortoises and small
516 vertebrates: success of barrier fences and culverts. Pp 169–173 In Trends in
517 addressing transportation related wildlife mortality: Proceedings of the
518 transportation related wildlife seminar. Evink, G.J., P. Garrett, D. Zeigler, and J.
519 Berry (Eds.). Environmental Management Office, Department of Transportation,
520 Tallahassee, Florida, USA.

521

522 Brooks, R. J., G. P. Brown, and D. A. Gailbraith. 1991. Effects of a sudden increase in
523 natural mortality of adults on a population of the common snapping turtle
524 (*Chelydra serpentina*). Canadian Journal of Zoology 69: 1314-1320.

525

526 Burger, J. and W.A. Montevecchi. 1975. Nest site selection in the Terrapin *Malaclemys*
527 *terrapin*. American Society of Ichthyologists and Herpetologists 1975:113–119.

528

529 Butler, J.A., C. Broadhurst, M. Green, and Z. Mullin. 2004. Nesting, nest predation and
530 hatchling emergence of the Carolina Diamondback Terrapin, *Malaclemys terrapin*
531 *centrata*, in Northeastern Florida. *American Midland Naturalist* 152:145–155.
532

533 Congdon, J.D., A.E. Dunham, and R.C. Van Loben Sels. 1993. Delayed sexual maturity
534 and demographics of Blanding’s Turtles (*Emydoidea blandingii*): Implications for
535 conservation and management of long-lived organisms. *Conservation Biology*
536 7:826–833.
537

538 Dodd, K.C., W.J. Barichivich, and L.L. Smith. 2004. Effectiveness of a barrier wall and
539 culverts in reducing wildlife mortality on a heavily traveled highway in Florida.
540 *Biological Conservation* 118:619–631.
541

542 Dorcas, M.E., J.D. Wilson, and J.W. Gibbons. 2007. Crab trapping causes population
543 decline and demographic changes in diamondback terrapins over two decades.
544 *Biological Conservation* 137:334–340.
545

546 Ernst, C.H., J.E. Lovich, and R.W. Barbour. 1994. *Turtles of the United States and*
547 *Canada*. Smithsonian Institution Press, Washington, D.C., USA.
548

549 Ernst, C.H., and R.W. Barbour. 1989. *Turtles of the World*. Smithsonian Institution Press,
550 Washington, D.C., USA.
551

552 Feinberg, J. A., and R. L. Burke. 2003. Nesting ecology and predation of Diamondback
553 Terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New
554 York. *Journal of Herpetology* 37:517-526.
555

556 Gibbons, J. W. 1986. Movement patterns among turtle populations: applicability to
557 management of the desert tortoise. *Herpetologica* 42:104-113.
558

559 Gibbons, J.H., J.E. Lovich, A.D. Tucker, N.N. Fitzsimmons, and J.L. Greene. 2001.
560 Demographic and ecological factors affecting conservation and management of
561 the Diamondback Terrapin (*Malaclemys terrapin*) in South Carolina. *Chelonian*
562 *Conservation and Biology* 4:66–74.
563

564 Gibbs, J.P., and G.D. Amato. 2000. Genetics and demography in turtle conservation. Pp
565 207–217 *In* *Turtle Conservation*. Klemens, M.W. (Ed.). Smithsonian Institution
566 Press, Washington, D.C., USA.
567

568 Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle
569 populations. *Conservation Biology* 16:1647–1652.
570

571 Goodwin, C.C. 1994. Aspects of nesting ecology of the diamondback terrapin
572 (*Malaclemys terrapin*) in Rhode Island. M.Sc. Thesis, University of Rhode Island,
573 Kingston, Rhode Island, USA. 84 p.
574

575 Grosse, A.M., J.C. Maerz, J. Hepinstall-Cymerman, and M.E. Dorcas. 2011. Effects of
576 roads and crabbing pressures on Diamondback Terrapin populations in coastal
577 Georgia. *Journal of Wildlife Management* 75:762–770.

578

579 Grottola, J.M., and R.C. Wood. March 2010. Atlantic Estuarine Research Society
580 meeting, Atlantic City, NJ. Saved from the Sewers: Rescuing hatchling
581 Diamondback Terrapins (*Malaclemys terrapin terrapin*) from storm drains along
582 the southern New Jersey coast.

583

584 Guyot, G., and J. Clobert. 1997. Conservation measures for a population of Hermann’s
585 Tortoise *Testudo hermanni* in southern France bisected by a major highway.
586 *Biological Conservation*. 79:251–256.

587

588 Hayward, M.W., and G.I.H. Kerley. January 2009. Fencing for conservation: Restriction
589 of evolutionary potential or a riposte to threatening processes? *Biological*
590 *Conservation*. 142:1–13.

591

592 Heppell, S. S., C. J. Limpus, D. T. Crouse, N. B. Frazer, and L. B. Crowder. 1996.
593 Population model analysis for the Loggerhead Sea Turtle, *Caretta caretta*, in
594 Queensland. *Wildlife Research*. 23:143-159.

595

596 James, A.N., K.J. Gatson, and A. Balmford. 1999. Balancing the Earth’s accounts.
597 *Nature*. 401:323–324.

598

599 Jaeger, J.A.G., and L. Fahrig. 2004. Effects of road fencing on population persistence.

600 Conservation Biology. 18:1651–1657.

601

602 Law, B.S., and C.R. Dickman. January 1998. The use of habitat mosaics by terrestrial

603 vertebrate fauna: implications for conservation and management. Biodiversity &

604 Conservation. 7:323–333.

605

606 Lovich, J.E. 1995. Turtles. Pp. 118–121 *In* Our Living Resources: A Report to the Nation

607 on the Distribution, Abundance, and Health of U.S. Plants, Animals, and

608 Ecosystems. Laroe, E.T., G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac

609 (Eds.). Department of the Interior, National Biological Service, Washington,

610 D.C., USA.

611

612 McLaughlin, D. 2011. The Wildlife Conservation Society meeting, New Jersey Chapter,

613 Waretown, New Jersey, USA. Research and management of diamondback

614 terrapins (*Malaclemys terrapin terrapin*) in New Jersey.

615

616 Pressey, R.L. 1994. Ad hoc reservation: forward or backward steps in developing

617 representative reserve systems. Biological Conservation. 8:662–668.

618

619 Roosenburg, W.M. 1991. Final report: the Chesapeake diamondback terrapin

620 investigations. Chesapeake Research Consortium Report 140. 24 p.

621

622 Roosenburg, W.M. 1994. Nesting habitat requirements of the diamondback terrapin: a
623 geographic comparison. *Wetland Journal*. 6:8-11.

624

625 Roosenburg, W.M., and A.R. Place. 1994. Nest predation and hatchling sex ratio in the
626 diamondback terrapin: implications for management and conservation. Pp. 65–70
627 *In Chesapeake Research Consortium Publication Number 149.*

628

629 Seigal, R.A., and J.W. Gibbons. 1995. Workshop on the ecology, status, and management
630 of the diamondback terrapin (*Malaclemys terrapin*). Savannah River Ecology
631 Laboratory: final results and recommendations. *Chelonian Conservation and*
632 *Biology* 1:240–243.

633

634 Silliman, B.R., and M.D. Bertness. 2002. A trophic cascade regulates salt marsh primary
635 production. *Proceedings of the National Academy of Science* 99:10500–10505.

636

637 Steen, D. A., and J. P. Gibbs. 2004. Effects of roads on the structure of freshwater turtle
638 populations. 2004. *Conservation Biology* 18:1143-1148.

639

640 Wilbur, H.M., and P.J. Morin. 1988. Life history evolution in turtles. Pp. 387–439 *In*
641 *Biology of the Reptillia*. Gans, C. and R.B., Huey (Eds.). John Wiley & Sons,
642 Inc., New York, New York, USA.

643

644 Wood, R.C. 1997. The impact of commercial crab traps on Northern Diamondback
645 Terrapins, *Malaclemys terrapin terrapin*. Pp.21–27 *In Proceedings: Conservation,*
646 *Restoration and Management of Tortoises and Turtles- An International*
647 *Conference.* Van Abbema, J. (Ed.). New York Turtle and Tortoise Society, New
648 York, New York, USA.

649

650 Wood, R.C., and R. Herlands. 1997. Turtles and tires: the impact of road kills on
651 Northern Diamondback Terrapin, *Malaclemys terrapin terrapin*, populations on
652 the Cape May Peninsula, southern New Jersey, USA. Pp.46–53 *In Proceedings:*
653 *Conservation, Restoration and Management of Tortoises and Turtles- An*
654 *International Conference.* Van Abbema, J. (Ed.). New York Turtle and Tortoise
655 Society, New York, New York, USA.

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658 **Figure Legends**

659

660 Figure 1. Map of two study sites in New Jersey, USA. Atlantic County and Cape May
661 County are outlined in red on the inset state map.

662

663 Figure 2. Predated and abandoned terrapin nests reflect nesting activity by indicating
664 where terrapins chose to lay eggs. Predated nests (a) are identified by eggshells scattered
665 nearby a shallow circular excavation. Abandoned nests (b) appear as shallow, circular
666 excavations.

667

668 Figure 3. Distribution of terrapin nests on SHB in 2011 (a) and 2012 (b) and MC in 2011
669 (c) and 2012 (d). Points are randomly jittered along both axes to allow the display of
670 overlapping data.

671

672 Figure 4. Straight-line distance to the free-ends of the fence on both roads. Distribution
673 of Stone Harbor Boulevard marsh-side nests (a) and road-side nests (b) used to generate
674 the expected distribution of marsh-side nest distances through Monte Carlo resampling
675 (c). Distribution of Margate Causeway marsh-side nests (d) and road-side nests (e) used
676 to generate the expected distribution of marsh-side nests as above (f). The vertical
677 dashed lines in (c) and (f) represent the observed median road-side nest distance to the
678 closest free end of the fence for each study site respectively for comparison to the
679 simulated distributions of nest distances.

680

681 Figure 5. Number of predated and abandoned nests on the Margate Causeway in 2011
682 and 2012 (a) and on Stone Harbor Boulevard in 2011 and 2012 (b) show an interaction
683 effect between year and site.

684

685 Figure 6. Terrapin escape success increases with size of gap beneath the fence. Black
686 sections of bars represent successful terrapin escape. White sections of bars represent
687 terrapin escape failure. Number of trials at a given size class is at the top of each bar.

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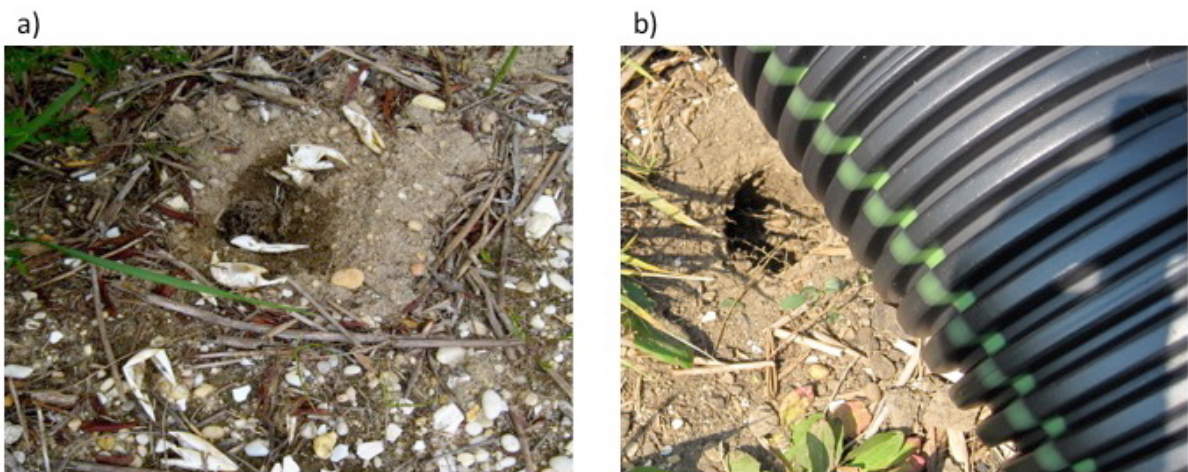
690 **Figures**

692 Figure 1



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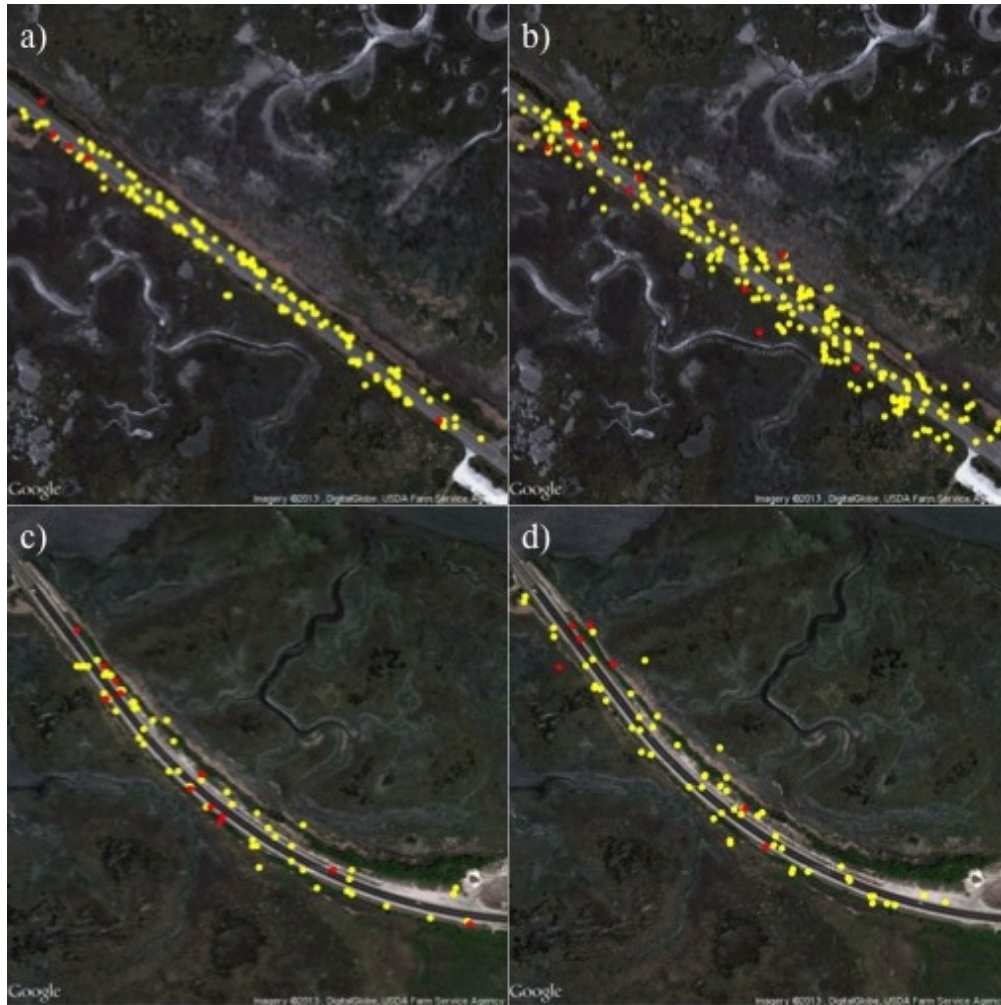
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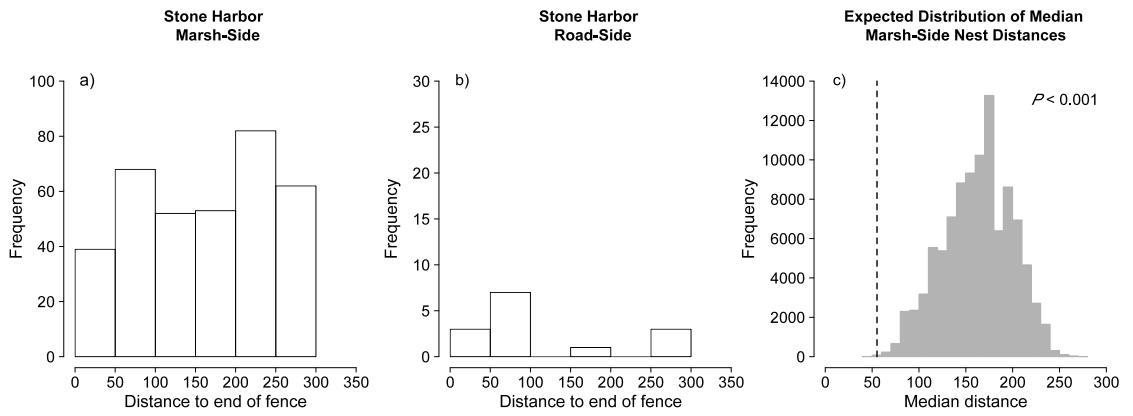
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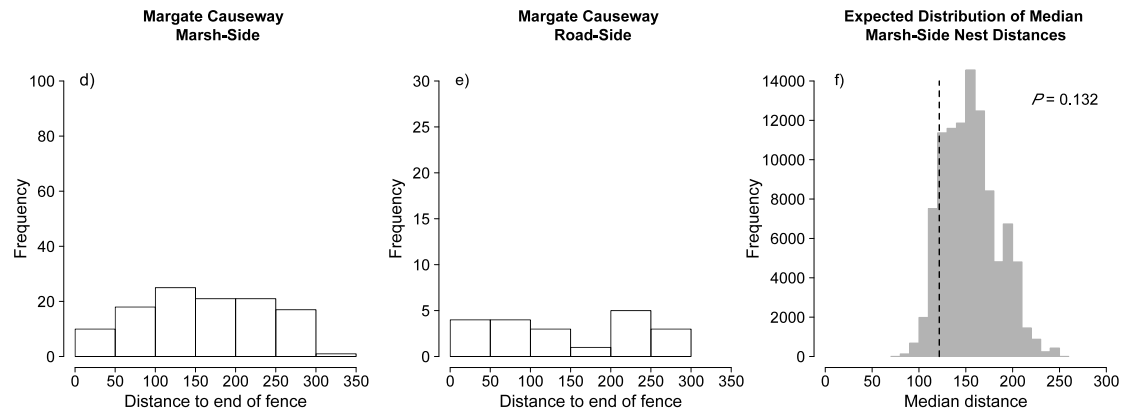
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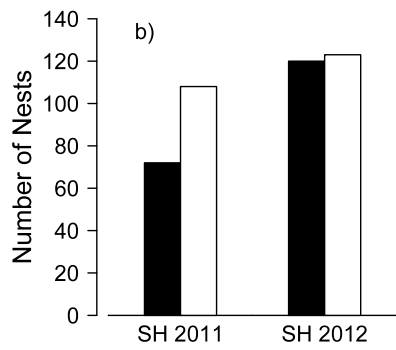
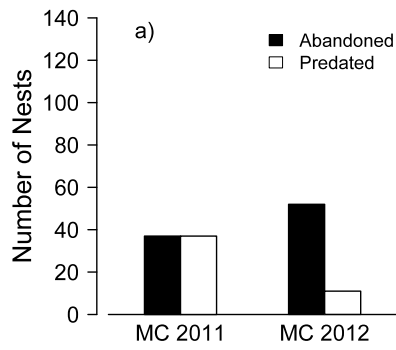
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821 Figure 6

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