Research Article

Presence of Ghost Crabs and Piping Plover Nesting Success

EUNBI KWON [iD],[1] *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24060, USA*

JAMES D. FRASER [iD], *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24060, USA*

DANIEL H. CATLIN [iD], *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24060, USA*

SARAH M. KARPANTY [iD], *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24060, USA*

CHELSEA E. WEITHMAN, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24060, USA*

BRITTA MUIZNIEKS,[2] *National Park Service, Cape Hatteras National Seashore, Manteo, NC 27954, USA*

ABSTRACT Despite intensive management to protect the federally threatened piping plover (*Charadrius melodus*), breeding success in North Carolina has consistently been lower than in other Atlantic Coast states. The native ghost crab (*Ocypode quadrata*) preys on plover eggs and chicks, but the effect of ghost crab predation on plover productivity has not been established. We used daily records of nest survival collected at Cape Hatteras National Seashore, North Carolina, USA from 2008 to 2015 to test a hypothesized negative relationship between the presence of ghost crabs within the 3-m diameter nest exclosure and the daily nest survival of plovers. We detected ghost crabs or their burrows within the nest exclosure on 63 out of 2,347 nest visits (24 out of 94 nests, 25%). We determined 9 nests (9.6%) were depredated by ghost crabs and 2 nests were abandoned after ghost crab visits. The estimated daily survival rate (DSR) of plover nests decreased with nest age, so to compare the nesting success predicted by our model, we standardized age in the prediction as the age at mid-incubation. At mid-incubation (nest age = 19 days), the DSR of a nest found with evidence of ghost crabs was 0.92 (95% CI = 0.74–0.98), compared to DSR of nests without ghost crabs (0.99, 95% CI = 0.97–0.99). We tested other covariates (e.g., clutch size, breeding timing, daily weather conditions); however, the standardized effect size of the presence of ghost crab was more than twice that of all other covariates. Ghost crabs may have a previously under-recognized effect on plover nest survival when avian and mammalian predation is precluded by nest exclosures. Protection of piping plover nests from ghost crabs may improve piping plover nest success. © 2018 The Wildlife Society.

KEY WORDS Cape Hatteras National Seashore, *Charadrius melodus*, egg predation, ghost crab, nest success, *Ocypode quadrata*, piping plover, reproductive success, shorebird.

Fecundity and survival are key determinants of the size, trend, and viability of populations. Therefore, management efforts for an imperiled species such as the piping plover (*Charadrius melodus*; plover) may focus on maintaining high reproductive output (number of offspring produced/breeding pair) and survival (U.S. Fish and Wildlife Service [USFWS] 1996). Since listing under the Endangered Species Act in 1986, plovers have been intensively managed and monitored throughout their Atlantic Coast breeding range, from Canada to North Carolina, USA (Haig and Oring 1985, USFWS 1996, Hecht and Melvin 2009).

Piping plover reproductive output in North Carolina is consistently lower than in other states in the Atlantic Coast range (USFWS 2016). The breeding population on Cape Hatteras National Seashore (CAHA) fluctuated between 2 and 15 breeding pairs/year from 1985–2016 (National Park Service [NPS], unpublished data). Reviews of the status of plovers at CAHA identified habitat loss and degradation, avian and mammalian predation, and disturbance by humans and dogs as key threats (USFWS 1996, 2009; Cohen et al. 2010).

Common predators of plover eggs include a variety of wild and domestic mammals and birds (MacIvor et al. 1990, Rimmer and Deblinger 1990, Mayer and Ryan 1991, Melvin et al. 1992, Cohen et al. 2010). Coordinated protective measures were implemented at CAHA, including installation of fences around nests (i.e., predator exclosures) to deter avian and mammalian predators, occasional removal of potential avian and mammalian predators, and complete or partial closure of nesting and brood-rearing areas to pedestrians and off-road vehicles (NPS 2007, 2010). However, the 5-cm × 10-cm mesh of predator exclosures do not exclude small mammals or burrowing predators such as ghost crabs (*Ocypode quadrata*).

Ghost crabs are native to plover habitat and occur on the western Atlantic Coast from Rhode Island, USA to Brazil, and throughout the Caribbean (Chace and Hobbs 1969). They feed on benthic deposits, detritus, and carrion, and actively prey on invertebrate and vertebrate animals (Strachan et al. 1999, Trott 1999, Hitchins et al. 2004, Chartosia et al. 2010, Lucrezi and Schlacher 2014). Live caught mole crabs (*Emerita talpoida*) and coquina clams (*Donax variabilis*) comprised 91% of ghost crab diets in North Carolina (Wolcott 1978). More than 40 taxa are ghost crab prey, including eggs of all 7 extant sea turtle species (Family Cheloniidae and Dermochelyidae) and several bird species that nest on beaches and dunes (Lucrezi and Schlacher 2014). Wolcott and Wolcott (1999) concluded that ghost crabs were not predatory threats to plovers, and suggested that ghost crabs may affect the survival of eggs and chicks indirectly by eliciting adult protective behavior that attracts other predators or prevents young from feeding efficiently. However, this does not explain eggs missing within predator exclosures.

Every plover nest found on CAHA since 1992 received a predator exclosure as soon as adults started to incubate their clutch. However, on average only half of nests successfully hatched each year on CAHA during 1999–2015 (NPS, unpublished data), lower than the 60–92% hatching success reported for exclosed nests in Massachusetts, Colorado, and North Dakota, USA (Rimmer and Deblinger 1990, Melvin et al. 1992, Mabee and Estelle 2000, Ivan and Murphy 2005). The objective of our study was to test our hypothesis that the presence of ghost crabs within predator exclosures will lower the daily nest survival of plovers at CAHA.

STUDY AREA

Cape Hatteras National Seashore is a 110-km long chain of barrier islands in the Outer Banks of North Carolina (35° 18′ N, 75° 30′ W; 122.83 km²). It is comprised of Bodie, Hatteras, and Ocracoke Islands, which are disconnected at Oregon and Hatteras inlets. Monthly average temperatures for March–July ranged from mid to upper 20°C during our study period. Daily peak wind gusts ranged from 3–44 m/second throughout the year with a mean gust of 11 m/second. Elevation ranged from sea level to 11 m, and the primary dunes were anthropogenically managed by construction and vegetative stabilization. Upper beach was sparsely covered with American sea rocket (*Cakile edentula edentula*), and dune slopes were vegetated with sea oats (*Uniola paniculata*), shore little bluestem (*Schizachyrium littorale*), saltmeadow cordgrass (*Spartina patens*), largeleaf pennywort (*Hydrocotyle bonariensis*), firewheel (*Gaillardia pulchella*), lanceleaf greenbrier (*Smilax smallii*), and prickly pear cactus (*Opuntia pusilla*). Providing a high-energy beach and dynamic barrier island habitat, the study area was inhabited by diverse species of shorebirds and sea turtles that were federally endangered or threatened. Required by laws and policies (the Migratory Bird Treaty Act, the Endangered Species Act, and NPS Management Policies), the NPS conducts resource management for the protected species and simultaneously manages the seashore for recreational uses.

Additionally, a high priority is placed on using the dune system to protect North Carolina Highway 12; dune blowouts that threaten the road are quickly patched.

METHODS

Plovers breed at CAHA from April to August, building nest scrapes on sandy dunes and overwash fans on open or sparsely vegetated beaches. Plovers typically lay a clutch of 3–4 eggs, and males and females incubate the eggs (Elliott-Smith and Haig 2004). Mating season of ghost crabs in North Carolina spans from June to September, and eggs released into the ocean develop through a pelagic larval stage and recruit back to the beach from July to September (Smith 1873, Lucrezi and Schlacher 2014). In North Carolina, ghost crabs build burrows that are 2–7.5 cm in diameter (Allen and Curran 1974). Body size of ghost crabs increases from June and peaks in August (overlapping with the plover breeding season), with carapace length ranging from 10 to 50 mm (Wolcott 1978, Hobbs et al. 2008).

Field Observations

Employees from NPS conducted plover nest monitoring at CAHA and monitoring began annually in early March. Although monitoring at CAHA started in 1985, we used only data from 2008–2015 because detailed accounts of daily observations were available for this period. Observers found nests by walk-through surveys and by observing plover behavior. Most nests were found during laying ($n = 85$), but some were found during incubation ($n = 26$). We observed every nest in the morning and in the evening for up to 1 hour/visit or until a nest exchange took place, whichever came first. We recorded onset of incubation, clutch size, and the nest fate. For every visit, we recorded the number of ghost crabs or openings of ghost crab burrows in the exclosure, signs of other predators, and the type and frequency of human disturbance near the exclosure. From 53 nests where the onset of incubation was observed and then monitored until successful hatching, we estimated the mean length of the incubation period to be 26 ± 1.96 (SD) days. We calculated nest age as the number of days since the first egg was laid for each nest. For 11 nests, we knew the day the first egg was laid. For all other nests, we estimated the date the first egg was laid using the observed date of onset of incubation ($n = 44$), observed date when the last egg was laid ($n = 27$), observed hatch date ($n = 15$), or expected hatch date from the egg floatation method ($n = 5$; Liebezeit et al. 2007). We assumed the interval between 2 eggs laid was 1.5 days and incubation period was 26 days when backdating the estimated lay day for nests found at later stages.

When each nest had ≥3 eggs, or when the clutch was complete, we installed a predator exclosure. Exclosures were circular, approximately 3 m in diameter, and consisted of 5-cm × 10-cm welded-wire fence topped with a 2-cm mesh netting (USFWS 1996). We classified nest fate as hatched, failed, abandoned, or unknown. We determined cause of failure or nest abandonment based on evidence at the site. We excluded nests from analyses if it failed before predator exclosures were installed. Field monitoring of piping plovers
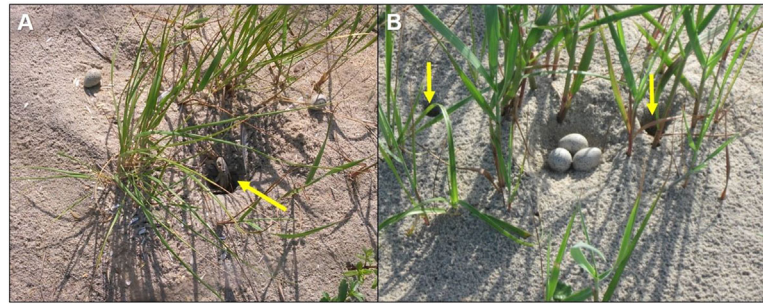
Figure 1. Evidence of ghost crabs and their burrows found within predator exclosures on nests of piping plover at Cape Hatteras National Seashore, North Carolina, USA, 2016. Arrows indicate crab burrows. A) Ghost crab burrowed in the nest cup and 2 eggs found rolled outside of the nest cup. B) Two burrows of ghost crabs appeared next to the plover nest. Photo credit: Paul Doshkov, National Park Service.

and installation of predator exclosures was approved by the Endangered Species Permit issued from North Carolina Wildlife Resources Commission (permit number 16-ES00197).

Statistical Analyses

We used logistic-exposure models to estimate daily nest survival rate and to examine a set of ecological and environmental covariates (Rotella et al. 2004, Shaffer 2004). Ecological covariates included reproductive stage (laying vs. incubation), nest age (number of days since clutch initiation), date, relative breeding phenology (the date of clutch initiation centered to the annual mean), clutch size, presence of predator exclosure (exclosed vs. not exclosed), and presence of ghost crab signs (present vs. absent). Environmental covariates included daily maximum temperature, daily fastest 2-minute wind speed, and daily total precipitation. All ecological and environmental covariates were occasion-specific except for relative breeding phenology and clutch size. Daily weather variables were measured at the Cape Hatteras Billy Mitchell Field, North Carolina (35° 13′ N, 75° 37′ W; https://www.ncdc.noaa.gov). We also included 2 grouping covariates: subsite (Hatteras, Ocracoke, Bodie) and year. We modeled 5 interactions: nest age × reproductive stage, ghost crab × daily maximum temperature, ghost crab × predator exclosure, ghost crab × clutch size, and ghost crab × relative breeding phenology. We tested fit of the global model with a Hosmer and Lemeshow goodness-of-fit test (Hosmer et al. 2013).

Three covariates (date, relative breeding phenology, and daily maximum temperature) were significantly collinear (all $P < 0.05$ with Pearson correlation coefficients >0.7; Lance et al. 2006). Therefore, we compared all possible submodels, prohibiting pairs of collinear variables in the same model. We do not report the list of all tested submodels because our explorative approach produced 5,600 submodels. We standardized covariates by subtracting the mean and dividing by the standard deviation. We used Akaike's Information Criterion corrected for the small sample sizes (AIC_c) to compare submodels (Burnham and Anderson 2002). Models with $\Delta AIC_c < 2$ were candidates for the top model. Because submodels included interactive effects of multiple variables, we did not estimate relative importance or average beta

estimates. Instead, we present the set of competitive models with $\Delta AIC_c < 2$ and examined the likelihood estimates for candidate models and 95% confidence interval for each of the variables to verify the significance of different variables (Arnold 2010, Cade 2015). We used the model with the lowest AIC_c value in our model set to estimate parameters.

RESULTS

During 2008–2015, observers found 120 nests at CAHA and daily monitoring records ($n = 2,347$) were available for 94 of these nests. The mean interval between observations at a nest was 1.09 ± 0.50 days (range = 1–13 days). Observers found ghost crabs or burrows within the nest exclosure at 24 of 94 nests (26%, Fig. 1) on 46 out of 2,347 observation days (2%). Eight percent of nests with ghost crab sign were abandoned compared to 6% of nests without ghost crab sign ($\chi_1^2 = 0.14$, $P = 0.71$; Table 1). Eggs were rolled out of the nest cup and found near the opening of the burrow in 6 nests (6% of monitored nests; Fig. 1).

Of 17 nests lost to predation, 9 were lost to ghost crabs, and 1 each to a gull (*Laridae* sp.) and a mink (*Neovison vison*). Six nests were lost to unknown predators. At nests depredated by avian or mammalian predators, we did not detect ghost crabs or their burrows prior to predation. We found ghost crab burrows at 2 of the 6 nests lost to unknown species. However,

Table 1. Piping plover nests by hatching success (hatched vs. failed) and field determined cause of failure by presence of ghost crab sign (none observed vs. ghost crabs or burrows within the predator exclosure), Cape Hatteras National Seashore, North Carolina, USA, 2008–2015.

	Nests without ghost crab		Nests with ghost crab	
	n	%	*n*	%
Hatched vs. failed[a]				
Hatched	55	79	12	50
Failed	15	21	12	50
Total	70	100	24	100
Failure cause				
Abandoned	4	6	2	8
Depredated	8	11	9	38
Failed other cause	3	4	1	4
Total	15	21	12	50

[a] Hatched vs. failed by presence of crabs, $\chi_1^2 = 5.80$, $P = 0.02$.

Table 2. Best candidate models to test ecological and environmental covariates on the daily nest survival of piping plovers at Cape Hatteras National Seashore, North Carolina, USA, 2008–2015. Top model set is shown with difference in Akaike's Information Criterion (ΔAIC_c) < 2 ranked by descending model weight (ω_i). K = the number of parameters, logLik = log likelihood.

Model[a]	K	logLik	ΔAIC_c	ω_i
Crab+stage+district+year+age+clutch+temp+wind+crab clutch	17	−231.99	0.00[b]	0.22
Crab+stage+district+year+age+clutch+temp+wind	16	−233.12	0.23	0.19
Crab+stage+district+year+age+clutch+temp+wind+crab clutch+crab temp	18	−231.47	0.99	0.13
Crab+stage+district+year+age+clutch+temp+wind+crab temp	17	−232.59	1.19	0.12
Crab+stage+district+year+age+clutch+temp+wind+rain+crab clutch	18	−231.80	1.66	0.09
Crab+stage+district+year+age+clutch+temp+wind+exclosure+crab clutch	18	−231.93	1.90	0.08
Crab+stage+district+year+age+clutch+temp+wind+crab clutch+age stage	18	−231.93	1.92	0.08
Crab+stage+district+year+age+clutch+temp+wind+rain	17	−232.97	1.96	0.08

[a] Variables included in models: crab = presence of a ghost crab or burrow within the nest exclosure at the beginning of monitoring interval; stage = reproductive stage (laying vs. incubation); district = Bodie Island, Hatteras Island, Ocracoke Island; age = days after clutch initiation; clutch = clutch size; temp = daily maximum temperature; wind = daily fastest 2-minute wind speed; rain = daily precipitation; exclosure = presence of predator exclosure at the beginning of monitoring interval. Total model set included 5,600 submodels.
[b] Lowest value of AIC_c = 498.25.

there was no direct evidence to link ghost crab presence and egg predation in these 2 nests (e.g., ghost crab tracks leading from their burrow to plover nests or plover eggs rolled closed to burrow entrances).

Our global model fit the data ($\chi^2_8 = 13.37$, $P = 0.10$). Eight covariates were included in all 8 competitive models (Table 2). The interaction term between presence of ghost crab × clutch size was included in 5 of 8 competitive models including the top model (cumulative weight = 0.52).

Plover nests had a significantly lower chance of surviving an interval between our nest visits (mean length = 1.1 ± 0.5 days) when we detected ghost crabs or their burrows near the nest cup ($\beta = -1.72$, 95% CI = -2.98 to -0.45; Fig. 2). The only predictor that showed a stronger effect on nest survival was breeding stage, with higher survival during the laying period than during the incubation period (breeding stage $\beta = 2.42 \pm 1.06$ vs. presence of crabs -1.72 ± 0.65; Fig. 2).

For both groups of nests (with and without crab sign), daily survival rate decreased as the nest age increased ($\beta = -0.50$, 95% CI = -0.08 to -0.18; Fig. 3) and was lower for nests with fewer eggs ($\beta = 0.48$, 95% CI = 0.26 -0.69; Fig. 4). The trend of lower nest survival with smaller clutches was stronger when there were ghost crabs present; however, the interactive effect was not significant ($\beta = 0.45$, 95% CI = -0.16–1.07; Fig. 4). Daily nest survival also decreased with faster ambient wind speed ($\beta = -0.26$, 95% CI = -0.49 to -0.03) but increased with warmer temperature ($\beta = 0.33$, 95% CI = 0.03–0.62). At CAHA, 86% of nests were protected with predator exclosures for 8 years, but our best model did not include the effects of predator exclosures (Table 2).

DISCUSSION

In congruence with our hypothesis, survival of plover nests was negatively related to the presence of ghost crab sign. Daily nest survival rate decreased as nests aged and was lower for nests with fewer eggs. Similar trends with the nest age and clutch size have been shown for the Great Plains population of plovers (Catlin et al. 2015). Additionally, lower temperature and higher wind speed were correlated

with lower daily survival rates. However, the effect size of the presence of ghost crabs was more than twice that of nest age, clutch size, or any of the daily weather conditions (Fig. 2).

With predator exclosures installed, 17 out of 94 nests were still lost to predation at CAHA. Ghost crabs depredated eggs on 9 nests of 17 nests depredated and 9.6% of all nests that we monitored. Even with the intensive field monitoring conducted at CAHA, we did not observe any direct ghost crab predation at the nest. Ghost crabs are nocturnal foragers (Clayton 2005, Valero-Pacheco et al. 2007), however, and all
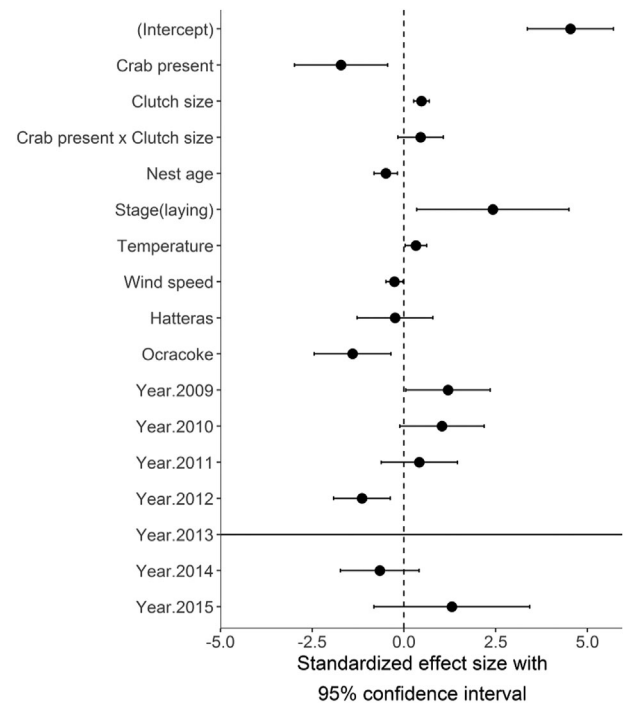

Figure 2. Standardized effect size (±95% CIs) on daily nest survival of piping plovers for covariates of interest from the best model. Absence of ghost crab was the baseline relative to presence of crab, incubation stage was the baseline relative to laying stage, subsite Ocracoke and year 2008 were the baseline for subsite (vs. Hatteras and Ocracoke) and year. In 2013, all 7 nests monitored on Cape Hatteras National Seashore, North Carolina, USA hatched ≥1 chick.
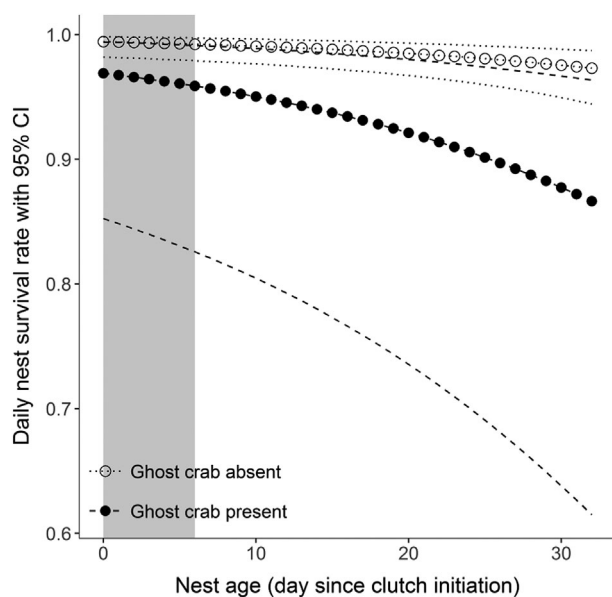
Figure 3. Predicted daily nest survival rates (±95% CIs) of piping plovers estimated throughout laying stage (nest age 0 to 6 days; shaded) and incubation stage (7 to 32 days) for nests with and without a ghost crab sign detected at the beginning of the monitoring interval at Cape Hatteras National Seashore, North Carolina, USA, 2008–2015.

our observations were during daylight. Seventy-one eggs were reported missing before hatch during our study, and 53 of those (75%) were reported on morning nest visits. Nocturnal foraging is typical for small mammals as well, and a previous study showed presence of white-footed mouse (*Peromyscus leucopus*), house mouse (*Mus musculus*), and rice rat (*Oryzomys palustris*) on CAHA (Oliver et al. 1999). Small mammals could potentially enter the predator exclosure and
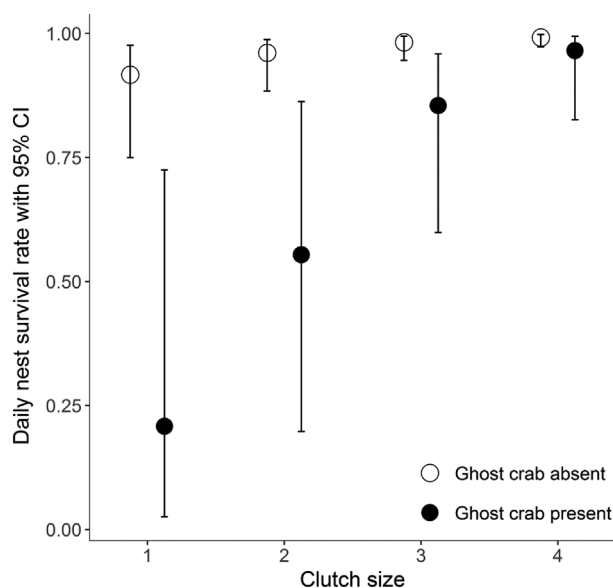
Figure 4. Predicted daily survival rates (±95% CIs) of piping plover nests by clutch sizes with and without a ghost crab sign, Cape Hatteras National Seashore, North Carolina, USA, 2008–2015.

eat eggs as seen at other sites (Lauro and Tanacredi 2002). However, these species typically inhabit densely vegetated areas and we did not detect any sign of small rodents at plover nests during our study period.

Predator exclosures effectively precluded large predators, such as raccoons (*Procyon lotor*), opossums (Didelphimorphia), and feral cats from accessing nests on CAHA. There were few other potential causes of missing eggs, which likely would have been detected: parents removing the eggs from the nest cup (Wiltermuth et al. 2009), flooding, or small-bodied predators other than ghost crabs (Lauro and Tanacredi 2002). Although we recorded all instances of ghost crab sign, the probability of finding a ghost crab burrow was greater for nests with missing eggs or missing birds because these signs called for close, physical examination of a nest. Therefore, it is possible that we undercounted ghost crab burrows when incubating plovers did not show any sign of disturbance. However, we physically checked all nests at least weekly in addition to monitoring daily from a distance. Because these weekly nest checks were spread out randomly in time and space, it should have reduced the probability that the significant effect of ghost crabs on nest survival was a complete artifact of a biased sampling. Ghost crabs build conspicuous burrows 2–7.5 cm wide in North Carolina (Allen and Curran 1974), and we detected at least 13 out of 65 burrows of ghost crabs while monitoring the nest from a distance with a field scope.

Wolcott and Wolcott (1999) argued that ghost crabs did not prey on eggs or chicks of plovers because they did not observe any predation by ghost crabs in the field or during a controlled experiment. In their study, plovers showed aggressive and exploratory behavior towards ghost crabs and their burrows (Wolcott and Wolcott 1999). Their results suggest that plovers perceive ghost crabs as a threat, which could lead to nest abandonment or increase flushing frequency, which might lead to loss of adults. However, in our study, only 2 of the 24 nests found with ghost crab burrows were abandoned, and the probability of nest abandonment was not significantly different between nests with and without ghost crabs. Furthermore, nest abandonment would not explain missing eggs because all nests were protected with predator exclosures at our site. Thus, our results suggest the negative effect of ghost crabs observed at CAHA is most likely a result of predation, not other disturbances.

In our study, ghost crabs preyed on 9.6% of monitored nest. Also at CAHA a least tern (*Sternula antillarum*) egg was taken by a ghost crab (M. D. Hillman, USFWS, personal communication), and we saw a ghost crab take a plover chick and drag it into a hole. On the Gulf Islands National Seashore in Florida, ghost crabs were responsible for 15% of snowy plover (*Charadrius nivosus*) nest loss and were the leading cause of predation on that site (Durkin 2012). In addition to taking eggs, ghost crabs were responsible for 12–24% of annual chick mortality of white-tailed tropicbirds (*Phaethon lepturus*) on Aride Island, Seychelles (Ramos et al. 2005). In other places, only single incidents have been reported (e.g., American oystercatcher chick [*Haematopus palliatus*], Georgia (Sabine et al. 2005); piping plover chicks,

Maryland (Loegering et al. 1995), Virginia [Watts and Bradshaw 1995]). Although limited to a single breeding population in North Carolina, our study clearly showed that ghost crabs can have an effect on plover nest survival when avian and mammalian predation is precluded with nest exclosures.

MANAGEMENT IMPLICATIONS

Protecting nests from ghost crabs could increase plover nest success at CAHA. Survival of pre-fledging chicks is, like nest success, a component of reproductive output. Chick survival at CAHA has often been <40% (NPS, unpublished data). The contribution of ghost crab predation to this low chick survival is unknown. If ghost crabs are influencing the high chick mortality, broad-scale removal of crabs from nesting beaches may increase reproductive output by protecting nests and chicks. However, before implementing large-scale removal of ghost crabs, a better understanding of the ecological role of ghost crabs in the beach ecosystem and the full effect of crabs on piping plover productivity is warranted. Ghost crabs prey on many species in addition to plovers, and are important prey of birds and mammals including some that also prey on plovers (Polis and Hurd 1996, Rose and Polis 1998, Barton and Roth 2008, Lucrezi and Schlacher 2014). Therefore, plans to control ghost crabs should be carefully evaluated for direct and indirect effects. Removal of ghost crabs also will require further studies on ghost crab movement ecology to adequately design and evaluate methods of ghost crab management.

ACKNOWLEDGMENTS

LITERATURE CITED

Allen, E. A., and H. A. Curran. 1974. Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. Journal of Sedimentary Research 44:538–548.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Barton, B. T., and J. D. Roth. 2008. Implications of intraguild predation for sea turtle nest protection. Biological Conservation 141:2139–2145.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Cade, B. S. 2015. Model averaging and muddled multimodel inferences. Ecology 96:2370–2382.

Catlin, D. H., J. D. Fraser, and J. H. Felio. 2015. Demographic responses of piping plovers to habitat creation on the Missouri river. Wildlife Monographs 192:1–42.

Chace, F. A., and H. H. Hobbs. 1969. The freshwater and terrestrial decapod crustaceans of the west Indies with special reference to Dominica. Smithsonian Institution, United States National Museum, Washington, D.C., USA.

Chartosia, N., M.-S. Kitsos, T. Tzomos, E. Mavromati, and A. Koukouras. 2010. Diet composition of five species of crabs (Decapoda: Brachyura) that show a gradual transition from marine to terrestrial life. Crustaceana 83:1181–1197.

Clayton, D. 2005. Substrate (acoustic/vibrational) communication and ecology of the ghost crab Ocypode jousseaumei (Brachyura: Ocypodidae). Marine and Freshwater Behaviour and Physiology 38:53–70.

Cohen, J. B., R. M. Erwin, J. B. French Jr., J. L. Marion, and J. M. Meyers. 2010. A review and synthesis of the scientific information related to the biology and management of species of special concern at Cape Hatteras National Seashore, North Carolina. U.S. Geological Survey Open-File Report 2009–1262. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Durkin, M. 2012. Distribution and dispersal of snowy plovers in Florida during the breeding and post-breeding period. Final Report to Edna Bailey Sussman Foundation. State University of New York, College of Environmental Science and Forestry, Syracuse, USA.

Elliott-Smith, E., and S. M. Haig. 2004. Piping plover (Charadrius melodus). Account 2 in P. G. Rodewald, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Haig, S. M., and L. W. Oring. 1985. Distribution and status of the piping plover throughout the annual cycle. Journal of Field Ornithology 56:334–345.

Hecht, A., and S. M. Melvin. 2009. Expenditures and effort associated with recovery of breeding Atlantic coast piping plovers. Journal of Wildlife Management 73:1099–1107.

Hitchins, P. M., O. Bourquin, and S. Hitchins. 2004. Nesting success of hawksbill turtles (Eretmochelys imbricata) on Cousine Island, Seychelles. Journal of Zoology 264:383–389.

Hobbs, C. H., C. B. Landry, and J. E. Perry. 2008. Assessing anthropogenic and natural impacts on ghost crabs (Ocypode quadrata) at Cape Hatteras National Seashore, North Carolina. Journal of Coastal Research 24:1450–1458.

Hosmer, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression. John Wiley and Sons, Hoboken, New Jersey, USA.

Ivan, J. S., and R. K. Murphy. 2005. What preys on piping plover eggs and chicks? Wildlife Society Bulletin 33:113–119.

Lance, C. E., M. M. Butts, and L. C. Michels. 2006. The sources of four commonly reported cutoff criteria: what did they really say? Organizational research methods 9:202–220.

Lauro, B., and J. Tanacredi. 2002. An examination of predatory pressures on piping plovers nesting at Breezy Point, New York. Waterbirds 25:401–409.

Liebezeit, J. R., P. A. Smith, R. B. Lanctot, H. Schekkerman, I. Tulp, S. J. Kendall, D. M. Tracy, R. J. Rodrigues, H. Meltofte, J. A. Robinson, C. Gratto-Trevor, B. J. Mccaffery, J. Morse, and S. W. Zack. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. The Condor 109:32–47.

Loegering, J. P., J. D. Fraser, and L. L. Loegering. 1995. Ghost crab preys on a piping plover chick. Wilson Journal of Ornithology 107:768–769.

Lucrezi, S., and T. A. Schlacher. 2014. The ecology of ghost crabs. Oceanography and Marine Biology: An Annual Review 52:201–256.

Mabee, T. J., and V. B. Estelle. 2000. Assessing the effectiveness of predator exclosures for plovers. Wilson Bulletin 112:14–20.

MacIvor, L. H., S. M. Melvin, and C. R. Griffin. 1990. Effects of research activity on piping plover nest predation. Journal of Wildlife Management 54:443–447.

Mayer, P. M., and M. R. Ryan. 1991. Electric fences reduce mammalian predation on piping plover nests and chicks. Wildlife Society Bulletin 19:59–63.

Melvin, S. M., L. H. MacIvor, and C. R. Griffin. 1992. Predator exclosures: a technique to reduce predation at piping plover nests. Wildlife Society Bulletin 20:143–148.

National Park Service [NPS]. 2007. Finding of no significant impact. Interim protected species management strategy/environmental assessment. Cape Hatteras National Seashore, North Carolina, USA.

National Park Service [NPS]. 2010. Cape Hatteras National Seashore off-road vehicle management plan/final environmental impact statement. Cape Hatteras National Seashore, North Carolina, USA.

Oliver, J. H. Jr., L. A. Magnarelli, H. J. Hutcheson, and J. F. Anderson. 1999. Ticks and antibodies to Borrelia burgdorferi from mammals at Cape Hatteras, NC and Assateague Island, MD and VA. Journal of Medical Entomology 36:578–587.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147:396–423.

Ramos, J. A., J. Bowler, M. Betts, C. Pacheco, J. Agombar, I. Bullock, and D. Monticelli. 2005. Productivity of white-tailed tropicbird on Aride Island, Seychelles. The International Journal of Waterbird Biology 28:405–410.

Rimmer, D. W., and R. D. Deblinger. 1990. Use of predator exclosures to protect piping plover nests. Journal of Field Ornithology 61:217–223.

Rose, M. D., and G. A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998–1007.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Sabine, J. B., J. M. Meyers, and S. H. Schweitzer. 2005. A simple, inexpensive video camera setup for the study of avian nest activity. Journal of Field Ornithology 76:293–297.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk: Ornithological Advances 121:526–540.

Smith, S. I. 1873. The megalops stage of Ocypoda. Annals and Magazine of Natural History 12:186–187.

Strachan, P. H., R. C. Smith, D. A. B. Hamilton, A. C. Taylor, and R. J. A. Atkinson. 1999. Studies on the ecology and behaviour of the ghost crab, *Ocypode cursor* (L.) in northern Cyprus. Scientia Marina 63:51–60.

Trott, T. J. 1999. Gustatory responses of ghost crab *Ocypode quadrata* to seawater extracts and chemical fractions of natural stimuli. Journal of Chemical Ecology 25:375–388.

U.S. Fish and Wildlife Service [USFWS]. 1996. Piping plover (*Charadrius melodus*), Atlantic coast population, revised recovery plan. USFWS, Hadley, Massachusetts, USA.

U.S. Fish and Wildlife Service [USFWS]. 2009. Piping plover (*Charadrius melodus*), 5-year review: summary and evaluation. USFWS, Hadley, Massachusetts, USA.

U.S. Fish and Wildlife Service [USFWS]. 2016. Estimated abundance of Atlantic coast piping plovers 1986–2014 and preliminary 2015 estimates. http://www.fws.gov/northeast/pipingplover. Accessed 24 Jul 2017.

Valero-Pacheco, E., F. Alvarez, L. G. Abarca-Arenas, and M. Escobar. 2007. Population density and activity pattern of the ghost crab, *Ocyposde quadrata*, in Veracruz, Mexico. Crustaceana 80:313–325.

Watts, B., and D. Bradshaw. 1995. Ghost crab preys on piping plover eggs. Wilson Journal of Ornithology 107:767–768.

Wiltermuth, M. T., M. J. Anteau, M. H. Sherfy, and T. L. Shaffer. 2009. Nest movement by piping plovers in response to changing habitat conditions. Condor: Ornithological Applications 111:550–555.

Wolcott, T. G. 1978. Ecological role of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: scavengers or predators? Journal of Experimental Marine Biology and Ecology 31:67–82.

Wolcott, D. L., and T. G. Wolcott. 1999. High mortality of piping plovers on beaches with abundant ghost crabs: correlation, not causation. Wilson Journal of Ornithology 111:321–329.

Associate Editor: Bill Block.