



RESEARCH ARTICLE

White-cheeked Pintail duckling and brood survival across wetland types at Humacao Nature Reserve, Puerto Rico

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ABSTRACT

Duckling survival is an important influence on recruitment in several North American *Anas* species. White-cheeked Pintail (*Anas bahamensis*) breeding in Puerto Rico encounter a variety of wetland types that may influence duckling survival. We monitored fates of 92 radio-tagged ducklings in 31 broods in 5 wetland habitat types at Humacao Nature Reserve in southeastern Puerto Rico from 2000 to 2002. Wetlands included 2 separate coastal lagoon complexes, mangrove forest, and managed and unmanaged wetland impoundments containing herbaceous vegetation. We used known-fate models to estimate daily and interval survival rates of ducklings and broods. We conducted conservative and liberal analyses of survival because of uncertain fates of 36 ducklings. In the conservative analysis, the most parsimonious model for duckling survival contained wetland type and a positive influence of daily precipitation. In the liberal analysis, duckling survival also varied among wetlands, was positively influenced by daily precipitation, but negatively influenced by hatch date. Brood survival was also positively influenced by precipitation and female body mass. Managed wetland impoundments and shallowly flooded lagoon habitats containing ferns, interspersed cattail (*Typha dominguensis*), and other herbaceous cover promoted up to 3 times higher survival of ducklings over the course of a 30-day duckling period than we found in mangroves, more deeply flooded lagoons with predominately restricted shoreline cover, or unmanaged impoundments overgrown with vegetation. Broad confidence intervals for survival estimates among wetlands preclude unequivocal interpretation, but our results suggest that White-cheeked Pintail ducklings survive poorly in mangroves but benefit from appropriate management.

Keywords: White-cheeked Pintail, *Anas bahamensis*, Humacao Nature Reserve, Puerto Rico, survival, brood, duckling

Supervivencia de juveniles y nidadas de *Anas bahamensis* en diferentes tipos de humedales en la Reserva Natural Humacao, Puerto Rico

RESUMEN

La supervivencia de los juveniles es una influencia importante en el reclutamiento de varias especies de *Anas* de América del Norte. *Anas bahamensis* se reproduce en Puerto Rico, donde encuentra una variedad de tipos de humedales que pueden influenciar la supervivencia de los juveniles. Seguimos el destino de 92 juveniles marcados con radios pertenecientes a 31 nidadas en cinco tipos de humedades en la Reserva Natural Humacao en el sudeste de Puerto Rico, desde 2000 hasta 2002. Los humedales incluyeron dos complejos separados de lagunas costeras, bosques de manglares y embalses manejados y no manejados con vegetación herbácea. Usamos modelos de supervivencia para estimar las tasas de supervivencia diaria e internas de los juveniles y las nidadas. Realizamos análisis conservadores y liberales de supervivencia debido al destino incierto de 36 juveniles. En los análisis conservadores, el modelo más parsimonioso para la supervivencia de los juveniles incluyó el tipo de humedal y una influencia positiva de la precipitación diaria. En los análisis liberales, la supervivencia de los juveniles también varió entre los humedales y estuvo positivamente influenciada por la precipitación diaria pero negativamente influenciada por la fecha de eclosión. La supervivencia de la nidada también estuvo positivamente influenciada por la precipitación y por la masa corporal de la hembra. Los hábitats de los embalses manejados y las lagunas inundables someras con presencia de helechos, *Typha dominguensis* y otra cobertura herbácea promovieron una supervivencia hasta tres veces mayor de los juveniles a lo largo del período juvenil de 30 días que lo que encontramos en los manglares, las lagunas inundables

más profundas con cobertura predominantemente restringida de la línea costera o embalses no manejados sobrepoblados de vegetación. Los intervalos de confianza generales de las estimaciones de supervivencia entre los humedales no permiten realizar una única interpretación, pero nuestros resultados sugieren que los juveniles de *A. bahamensis* presentan una baja supervivencia en los manglares pero son beneficiados por un manejo adecuado.

Palabras clave: *Anas bahamensis*, juvenil, nidada, Puerto Rico, Reserva Natural Humacao, supervivencia.

INTRODUCTION

Patterns and processes influencing demography are critical components of avian life histories. Lack (1954, 1966) proposed that changes in size of bird populations were determined by a combination of addition of new recruits into the population (density independence) and density-dependent mortality during the nonbreeding season, a hypothesis recently revalidated as an explanation for regulation and limitation of bird populations (Sæther et al. 2016). In dabbling ducks (Anatini), adult female survival, nest success, and duckling survival are primary influences of annual recruitment (Hoekman et al. 2002, Coluccy et al. 2008). Duck broods encounter variable wetland conditions, diverse and sometimes abundant predators, and other biotic and abiotic factors that affect survival of young (Johnson et al. 1989, 1992; Davis et al. 2007; Amundson and Arnold 2011).

Oceanic insular species of waterfowl and other wetland birds are vulnerable to introduced predators, to loss of coastal areas, ponds, and mangrove forests, and in some cases overharvesting (Sorenson 2005). Introduced mammals especially threaten endemic island species (Ebenhard 1988, Lever 1994, Brown 2012). Predation by introduced animals has been the cause of an estimated 42% of island bird extinctions worldwide (King 1985, Brown 2012). Snowy Plover (*Charadrius alexandrinus*), for example, has recently been extirpated from the Caribbean island of Saint Martin, attributed to human disturbance to nesting birds and predation by invasive species (Brown 2012). In the presence of predators, islands can be more perilous for nesting than mainland locations. For example, Lombard et al. (2010) estimated just 0.06 chicks fledging per nest attempt from 4,640 Least Tern (*Sterna antillarum*) nests across 56 colonies in the U.S. Virgin Islands, the lowest nesting success reported for this species anywhere in its range.

Compared to Nearctic Anatidae, Neotropical waterfowl such as the White-cheeked Pintail (*Anas bahamensis*) are less migratory and often have smaller annual ranges than most species of dabbling ducks, putting them at risk due to local-scale habitat change and predator introduction (Weller 1980, Baldassarre 2014). White-cheeked Pintail occur throughout the West Indies and South America, with *Anas bahamensis bahamensis* resident from the West Indies to northern South America (Raffaele 1998, Sorenson 2005). White-cheeked Pintails are classified as threatened in Puerto Rico by the Department of Natural

and Environmental Resources (García et al. 2005) but are considered a species of Least Concern across most of their range by the International Union for Conservation of Nature (BirdLife International 2012). Low White-cheeked Pintail populations in Puerto Rico and other Caribbean islands have prompted management concern (BirdLife International 2012).

The Humacao Nature Reserve (hereafter, Humacao) in Puerto Rico, nearby islands of Culebra and Vieques, and the Virgin Islands are key habitats for White-cheeked Pintails in the eastern Caribbean region (Collazo and Bonilla-Martínez 2001). Previous research has addressed nesting ecology, annual survival rates, density and population size, and adult movements of these ducks at Humacao and other coastal systems (López-Flores et al. 2014). López-Flores et al. (2014) quantified survival of brood-rearing White-cheeked Pintail females. They documented a high hen survival rate suggesting that adult female survival was not a bottleneck to recruitment at Humacao. Because duckling survival is an important influence of recruitment in dabbling ducks (Hoekman et al. 2002), our objective was to estimate survival of White-cheeked Pintail ducklings at Humacao. The setting at Humacao offered the opportunity to examine survival across multiple wetland types: palustrine emergent wetlands with shallow open water (≤ 20 cm) interspersed with cattail (*Typha dominguensis*) but lacking predatory fish (e.g., tarpon [*Megalops atlanticus*], common snook [*Centropomus undecimalis*]); wetlands (e.g., lagoons) that contained less vegetation, had deeper water, and contained fish; and mangroves. We hypothesized that survival of White-cheeked Pintail ducklings and broods would be greatest in seasonal–semipermanently flooded palustrine wetlands, based on previous studies of radio-tagged Nearctic ducks that linked survival to birds' use of hemi-emergent and semipermanent wetlands (Cowardin et al. 1979, Krapu et al. 2006). If certain wetland types influence duckling survival, particularly wetlands where vegetation and water management can be manipulated to benefit broods (e.g., hemi-marsh; Murkin et al. 1997), this could have important implications for White-cheeked Pintail populations.

METHODS

Study Area

Humacao is located in southeastern Puerto Rico (18.16°N, 65.77°W) on a coastal plain estuary formed by 3

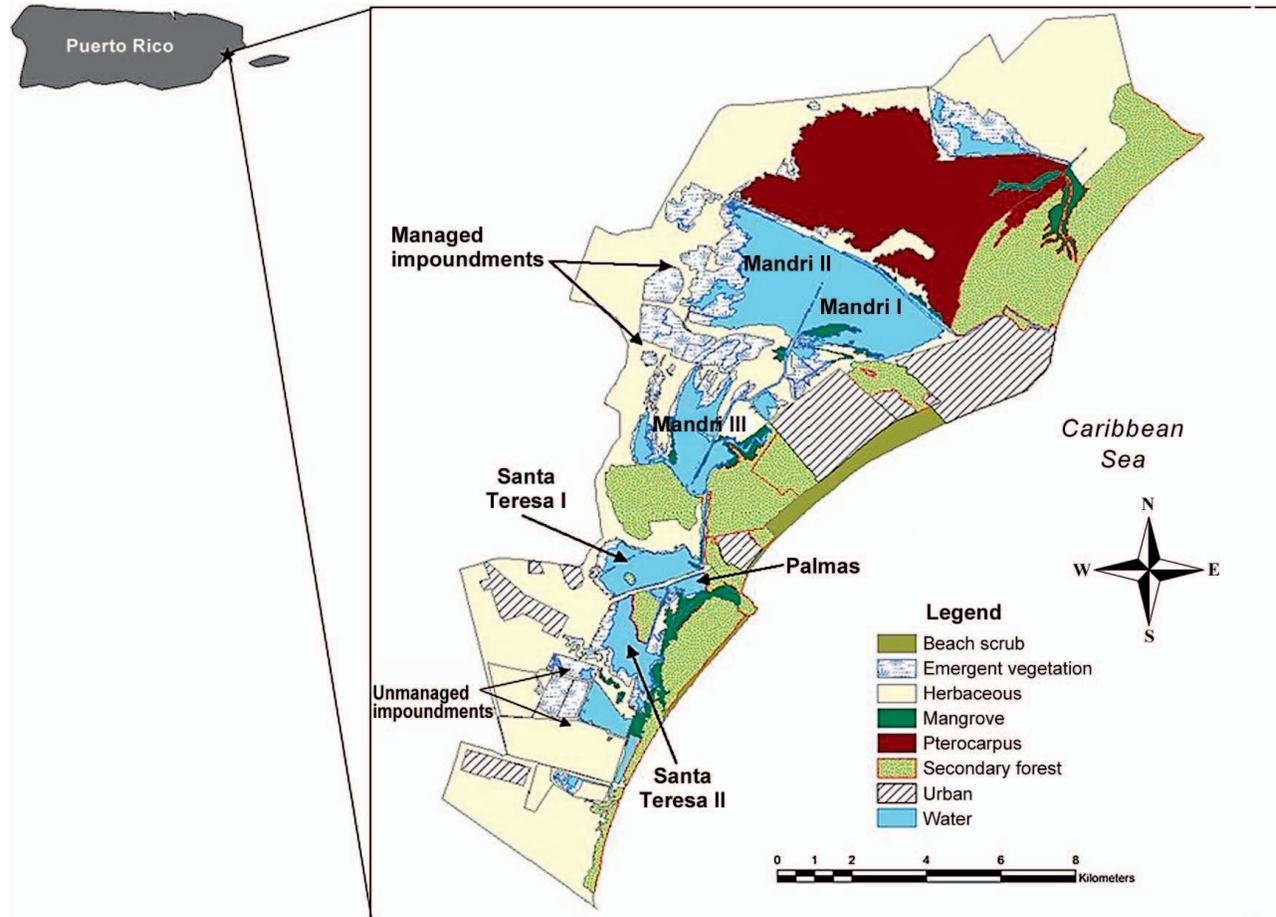


FIGURE 1. Major wetland habitats of the Humacao Nature Reserve, Puerto Rico.

interconnected drainages (Vilella and Gray 1997). The region was originally dominated by coastal wetlands before being cleared and drained for sugarcane (*Saccharum*) production in the 1920s. The area remained under sugarcane cultivation until Hurricane David and Tropical Storm Frederick struck Puerto Rico in 1979, causing extensive flooding. These storms collapsed the levee system and resulted in the establishment of estuarine lagoons and associated wetlands (Figure 1). Humacao coastal lagoons are composed of 2 major complexes located at opposite ends of the reserve: Santa Teresa (Santa Teresa I, Santa Teresa II, Palmas) and Mandri (Mandri I, Mandri II, and Mandri III). Due to the wetlands and wildlife values, the area was officially designated as a nature reserve in 1986 (Vilella and Gray 1997).

Six major wetland types (Figure 1) occurred at Humacao: (1) coastal lagoon (261 ha); (2) herbaceous emergent marsh (364 ha), which was composed of 3 managed impoundments; (3) 4 zones of mangrove forest (25.2 ha) including, in order of decreasing salt tolerance, red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia*

racemosa), and buttonwood mangrove (*Conocarpus erectus*); (4) forested wetlands (262 ha), largely swamp bloodwood (*Pterocarpus officinalis*), a leguminous tree that dominates fresh and brackish coastal regions of the Caribbean basin; (5) coastal forest (50 ha); and (6) beach scrub (4.4 ha).

Coastal forests were primarily found in higher elevations located on relict shorelines and fossil dunes, whereas lagoons and emergent wetlands predominated in areas with geological depressions and historically disturbed forested wetlands (Puerto Rico Department of Commerce and Department of Natural Resources 1986). Coastal lagoons were mostly surrounded by emergent vegetation, including cattail and aquatic ferns (*Acrostichum* spp.). Estuarine lagoons divided Humacao into 2 major lagoon complexes, Santa Teresa and Mandri (Figure 1). Water depths of lagoons ranged from 0.25 to 2.0 m, and salinity varied seasonally but increased during the dry season (Puerto Rico Department of Commerce and Department of Natural Resources 1986). Managed impoundments were constructed at Humacao in 1999 to restore abandoned sugarcane fields to emergent wetlands adjacent to the Mandri lagoon complex (Vilella and

Gray 1997). Managed impoundments typified moist-soil wetland complexes (Fredrickson and Taylor 1982, Kross et al. 2008) and were initially flooded in 2000 to provide habitat for resident and migratory wetland wildlife. Water flowed into Humacao from nearby rivers, fed by rainfall and saltwater intrusion. Seawater entered Humacao during periods of high precipitation (i.e. swells) and extreme overflow (Puerto Rico Department of Commerce and Department of Natural Resources 1986). Air temperature at Humacao is nearly constant throughout the year ($25 \pm 3^\circ\text{C}$; Ewel and Whitmore 1973, Rundle et al. 2002). Rainfall was quite variable at Humacao during our study but exhibited a bimodal relationship with the first peak occurring in April/May (11.2–18.9 cm) and the second peak generally occurring in August/September (15.5–27.8 cm). Between March and August rainfall ranged from 2.1 cm (March) to 25.4 cm (August) in 2000 (mean = 11.9 cm), 8.8 cm (March) to 23.4 cm (August) in 2001 (mean = 13.1 cm), and 3.8 cm (March) to 16.4 cm (May) in 2002 (mean = 11.9 cm).

Nest Searching

Artificial nest structures were deployed at Humacao in 1989 to increase waterfowl production, especially for White-cheeked Pintails (M. Córbet, Puerto Rico Department of Commerce and Department of Natural Resources, personal communication). Structures were 189-liter drums cut lengthwise, partially filled with sand to anchor on a soil substrate, and ultimately accreted soil and herbaceous vegetation (i.e. panic grass [*Panicum* spp.]) providing nest sites for White-cheeked Pintails. Wetland managers of the Department of Natural and Environmental Resources (DNER) at Humacao monitored and managed artificial nesting structures and natural nests in decayed coconut palm (*Cocos nucifera*) stumps annually to maintain their function for nesting White-cheeked Pintails (López-Flores 2005).

Using a kayak we searched for nesting White-cheeked Pintails in coastal lagoons (Palmas, Santa Teresa I and II, and Mandri I–III) from February to August 2000–2002 and managed impoundments from January to June 2001–2002 (Figure 1). We observed male behavior as a cue for detecting nests (Sorenson 1992, 2005); upon detecting the approximate location of a nest, we searched intensively in a 20 m radius. We also walked through vegetation from January to June searching for nests in vicinities of White-cheeked Pintail pairs. We focused our efforts on artificial structures because most White-cheeked Pintails use nesting structures (Bonilla-Martínez 1995). We candled several eggs in each nest to estimate hatch date (Weller 1956).

Radio-Tagging and Monitoring

We used a dip net (~0.6 m) with a pole (~1.5 m) to capture nesting female White-cheeked Pintails in artificial

structures or natural vegetation ~1 week before predicted hatching date. We radio-tagged females with prong-and-suture style VHF transmitter (Model 2032, Advanced Telemetry Systems, Isanti, Minnesota, USA) and returned them to the nest (Rotella and Ratti 1992; see also López-Flores 2005, López-Flores et al. 2014). During the 2000 pilot season, we only marked nesting females in June and July, while in 2001 and 2002 we marked and tracked birds from March through mid–late August. White-cheeked Pintails in Puerto Rico have been reported nesting in every month, but peak nesting occurs from March to July with a second, less pronounced nesting peak in October (Meier et al. 1989, Sorenson 1992).

On the expected day of hatch, we returned to the nest to capture and mark ducklings. We randomly selected 3 ducklings to which we applied a web-tag (Model 1005-1, National Band and Tag, Newport, Kentucky, USA) into the web of one foot, and attached a prong-and-suture transmitter (Davis et al. 2007). Duckling transmitters (Model 377, Advanced Telemetry Systems, Isanti, Minnesota, USA) weighed ~1.6 g and measured $17 \times 7.5 \times 8.8$ mm (Mauser and Jarvis 1991, Davis et al. 2007). Transmitter weight was ~6% of mean duckling body mass at hatch. Transmitters were expected to last 30 days (see López-Flores 2005, Davis et al. 2007). Beginning the day after transmitters were attached, we monitored females and broods daily via boat, kayak, or walking. We monitored birds until transmitters expired, females emigrated from the study area or died, or termination of the study in a given year (López-Flores 2005, Davis et al. 2007).

Explanatory Variables

We measured 3 categories of potentially important covariates to White-cheeked Pintail duckling and brood survival at Humacao: (1) adult female–related variables, (2) brood-related variables, and (3) environmental variables. We did not include a year term in our model set because of limited numbers of radio-tagged ducklings within years, particularly in the first year, which was largely a pilot study.

Female- and brood-related variables. We used female mass (~1 week before predicted hatching date), duckling mass on hatch day, ordinal hatch date of the first egg in the clutch, brood size, number of ducklings that exited the nest, determined directly or from eggshell membranes (Davis et al. 1998), and duckling age. We estimated the average inter-day movement distance of females and broods using the Animal Movements Extension (Hooge and Eichenlaub 1997) in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California, USA).

Environmental variables. We included daily precipitation from a National Weather Service weather station located at Humacao. We differentiated 5 wetland categories based on salinity, presence of artificial nesting structures, dominant vegetation, and wetland structure

(Figure 1): (1) Santa Teresa lagoons, composed of 3 coastal lagoons (Santa Teresa I and II, and Palmas) with >50% open water rimmed with cattail that were contiguous and amalgamated when water levels rose during the rainy season (Vilella and Gray 1997); (2) mangrove, an afforested wetland composed mainly of white mangrove and pond apple (*Annona glabra*), which was flooded year round except during droughts; (3) managed impoundments, located in northern Humacao, contained predominately moist-soil vegetation such as swamp flatsedge (*Cyperus ligularis*), sprangletop (*Leptochloa* sp.), millet (*Echinochloa colonum*), and others; (4) unmanaged impoundments, located at the southwestern end of Humacao typified by open water, cattail, and *Cyperus giganteus*; and (5) Mandri lagoon complex, which comprised the greatest area and was more saline than the Santa Teresa lagoons, despite similar vegetative composition and extent of open water. We assigned each daily location of radio-tagged ducklings to a specific wetland type after approaching the duckling by foot or boat.

Survival Estimation

Duckling survival. We calculated daily survival rates to 30 days post-hatch for radio-tagged ducklings using known-fate modeling in program MARK (White and Burnham 1999, Amundson and Arnold 2011). Duckling survival was calculated as the product of daily survival rates across 30 days. An important assumption of known-fate modeling is that survival of radio-tagged individuals is independent, which may be violated when multiple ducklings are marked in a brood (Chouinard and Arnold 2007). Program MARK does not support goodness-of-fit tests for known-fate models, and we did not have unbiased final numbers of surviving ducklings that would have enabled us to use Winterstein's (1992) second goodness-of-fit test (Chouinard and Arnold 2007; Schamber et al. 2009, 2010).

We had 36 radio-tagged ducklings for which we could not locate VHF signals for 30 days. We could not conclude for these birds if transmitters failed when ducklings used saltwater environments, failed for other reasons, or if signal loss was confounded with mortality (López-Flores 2005). Therefore, we conducted 2 separate versions of known-fate analysis to account for uncertainty in duckling fates (Hupp et al. 2007, Mateo-Moriones et al. 2012): (1) a conservative model, where we right-censored the 36 ducklings following signal loss and assumed that censored ducklings had similar survival rates as uncensored individuals; and (2) a liberal model, where we coded the last encounter with each of the lost 36 ducklings as a mortality event, thus assuming that signal loss was entirely due to mortality.

We right-censored ducklings in both conservative and liberal analyses when transmitters were known to be shed

or failed (Pollock et al. 1989a, 1989b; Davis et al. 2007). For survival analyses, beyond the 36 transmitters described above, we assumed censorship (e.g., transmitter loss or failure) was random and independent of fate of radio-tagged ducklings (Pollock et al. 1989a, 1989b; Bunck and Pollock 1993; Chouinard and Arnold 2007). We also assumed that survival of all birds was not affected by capture, handling, or radio-tags (Pollock et al. 1989a, 1989b; Davis et al. 2007).

Following Burnham and Anderson (1998) and Anderson et al. (2000), we developed a priori candidate models considering knowledge of duckling and brood survival from previous studies. Our primary goal was to develop a set of candidate models that would enable evaluation of important female-, brood-, and environment-related variables on survival. Our model set included a fully parameterized global model with 8 covariates of interest and 32 combinations of the following: wetland, hatch date, duckling mass, female mass, brood size, daily precipitation, average daily distance moved, and duckling age. We estimated duckling survival in wetlands by partitioning each duckling encounter history into segments based on occupied wetland type using left and right censoring (Pollock et al. 1989b, Chouinard and Arnold 2007). We initially modeled continuous effects of duckling age and identified periods of homogenous survival and incorporated these into 2 age classes in the known fate models (0–7 and 8–30 days post-hatch) to reduce parameter space (Chouinard and Arnold 2007). We selected among 33 parameterizations using Akaike's Information Criterion (AIC) adjusted for small sample size (AIC_c). We considered models within 2 Δ AIC_c as competitive so long as the parameterization of the subsidiary model was not the addition of a single parameter to the top model (Burnham and Anderson 2002, Arnold 2010). We report daily and derived survival rates with 95% confidence intervals (CI) and effect estimates ± 1 standard error.

Brood survival. We defined successful broods as those with at least one duckling surviving ≥ 30 days post-hatch and failed broods as those experiencing total brood loss <30 days post-hatch (Rotella and Ratti 1992, Saylor and Williams 1997, Dzus and Clark 1997, Davis et al. 2007). We used established criteria to designate total brood loss (i.e. no apparent living ducklings): (1) when we observed radio-tagged females repeatedly (i.e. ≥ 3 consecutive days) with neither marked nor unmarked ducklings; (2) when females emigrated from the study area; (3) when females without radio-tagged ducklings moved among wetlands daily and showed no affinity for sites, especially those used previously; or (4) when we observed females with a male within 2 weeks following brood exodus from nests (Bellrose and Holm 1994, Granfors 1996, Davis et al. 2007). We defined the brood-rearing period as ending with

TABLE 1. Most parsimonious and competing models for survival of 92 radio-tagged White-cheeked Pintail ducklings from 31 broods at Humacao Nature Preserve, Puerto Rico, from 2000 to 2002, using Akaike's Information Criterion (adjusted for small sample size; AIC_c). w_i = model weight, k = number of parameters.

Model	ΔAIC_c	w_i	k	Deviance
Conservative duckling survival ^a				
Wetland + Daily precip	0.00 ^c	0.49	6	345.27
Wetland + Duckling age _{0-7, 8-30}	1.14	0.28	6	346.41
Wetland	1.51	0.23	5	348.82
Liberal duckling survival ^b				
Wetland + Hatch date + Daily precip	0.00 ^d	0.48	7	492.24
Wetland + Hatch date	1.19	0.27	6	495.47
Wetland + Hatch date + Duckling mass + Female mass + Brood size + Daily precip + Avg. dist. moved	1.32	0.25	11	485.30
Brood survival				
Daily precip + Hatch date + Female mass	0.00 ^e	0.50	4	175.27
Female mass + Hatch date	1.22	0.27	3	178.54
Daily precip + Hatch date	1.53	0.23	3	178.85

^a Duckling survival using a conservative mortality estimate in which ducklings were considered alive at time of radio-tag signal loss and were right-censored thereafter.

^b Duckling survival using a liberal mortality estimate in which radio-tag signal loss was considered to be entirely confounded with mortality of the duckling.

^c The AIC_c value of the top conservative duckling survival model was 357.42.

^d The AIC_c value of the top liberal duckling survival model was 506.43.

^e The AIC_c value of the top brood survival model was 183.39.

female mortality, total brood mortality, or 30 days of age (Arnold et al. 2012).

We calculated brood survival to 30 days post-hatch using a known-fate analysis in program MARK (White and Burnham 1999). We included 7 covariates of interest in 23 models including a priori combinations of wetland, hatch date, female mass, brood size, daily precipitation, average daily distance moved, and brood age. Similar to duckling analyses, we partitioned encounter histories to evaluate wetland-specific brood survival, and incorporated 2 brood ages (i.e. 0–7 and 8–30 days post-hatch) to reduce parameter space of age effects. We selected among 23 parameterizations using AIC_c , and evaluated models of brood survival as we did for ducklings (Burnham and Anderson 2002, Arnold 2010).

RESULTS

We radio-tagged 93 White-cheeked Pintail ducklings at Humacao, including 15 ducklings marked from June 2 to July 14, 2000, 45 from March 28 to August 14, 2001, and 33 from March 18 to July 9, 2002. One radio failed in 2000; we excluded this duckling. Radio-tagged ducklings spent much more time in some wetlands than in others: mangrove wetland ($n = 229$ days), Santa Teresa lagoons ($n = 206$ days), unmanaged impoundments ($n = 150$ days), Mandri lagoon complex ($n = 107$ days), and managed impoundments ($n = 35$ days).

In the conservative analysis, 25 known mortalities occurred in the Santa Teresa lagoons, 17 in mangrove

wetlands, 1 in unmanaged impoundments, 4 in the Mandri lagoon complex, and 4 in managed impoundments. Of the 36 ducklings for which we were unable to reconcile true fates, 19 (53%) were last detected in the Santa Teresa lagoons before disappearing. Other lost transmitters were last detected in mangrove ($n = 7$, 19%), unmanaged impoundments ($n = 6$, 17%), Mandri lagoon complex ($n = 3$, 8%), and managed impoundments ($n = 1$, 3%).

Duckling Survival

Conservative estimate. Our conservative survival analysis included 51 ducklings with known mortalities, 36 ducklings that were right-censored following signal loss, and 5 ducklings that survived to 30-days post-hatch. The best daily survival model included daily precipitation and wetland ($w_i = 0.49$; Table 1). Daily precipitation was a positive predictor of duckling survival ($\beta = 0.46 \pm 0.28$). We estimated daily and interval survival rates of ducklings among wetlands by holding daily precipitation constant at its mean across all years (Table 2). Interval duckling survival ranged from 0.46 (95% CI = 0.17, 0.78) to 0.60 (95% CI = 0.21, 0.90) in managed impoundments and the Mandri lagoon complex, but was reduced to <0.16 in mangrove, unmanaged impoundments, and Santa Teresa lagoons (Table 2). We found 2 additional competitive models in the conservative duckling survival analysis, both with a wetland effect, but one also showing increased survival for ducklings 8–30 days of age ($\beta = 0.49 \pm 0.31$) (Table 1).

Liberal estimate. The liberal estimate of survival also included 92 ducklings; however, we classified 36 ducklings

TABLE 2. Daily and interval survival rates of White-cheeked Pintail ducklings ($n = 92$) at 5 wetlands at Humacao Nature Preserve, Puerto Rico, from 2000 to 2002. Values are survival estimates (with 95% CI in parentheses).

	Managed impoundments	Mandri complex	Mangrove	Unmanaged impoundments	Santa Theresa lagoons
Conservative^a					
Daily ^c	0.97 (0.93–0.99)	0.98 (0.94–1.00)	0.94 (0.90–0.96)	0.89 (0.75–0.96)	0.87 (0.82–0.91)
Precip 0 cm ^d	0.93 (0.92–0.99)	0.98 (0.92–0.99)	0.93 (0.88–0.96)	0.87 (0.70–0.95)	0.84 (0.77–0.90)
Precip 1.35 cm ^d	0.98 (0.95–0.99)	0.99 (0.95–1.00)	0.96 (0.91–0.98)	0.93 (0.79–0.98)	0.91 (0.84–0.95)
Interval (30 day) ^c	0.46 (0.17–0.78)	0.60 (0.21–0.90)	0.16 (0.06–0.38)	0.03 (0.00–0.53)	0.02 (0.00–0.08)
Liberal^b					
Daily ^c	0.94 (0.88–0.97)	0.94 (0.88–0.97)	0.90 (0.86–0.94)	0.82 (0.64–0.93)	0.81 (0.75–0.86)
Precip 0 cm ^d	0.93 (0.86–0.97)	0.93 (0.86–0.97)	0.89 (0.84–0.92)	0.80 (0.60–0.91)	0.78 (0.70–0.85)
Precip 1.35 cm ^d	0.95 (0.90–0.98)	0.95 (0.90–0.98)	0.92 (0.87–0.96)	0.86 (0.68–0.95)	0.85 (0.77–0.90)
Hatch–March 30 ^d	0.97 (0.93–0.98)	0.96 (0.92–0.98)	0.94 (0.90–0.97)	0.89 (0.76–0.96)	0.88 (0.80–0.93)
Hatch–July 16 ^d	0.91 (0.80–0.96)	0.91 (0.81–0.96)	0.85 (0.77–0.91)	0.74 (0.49–0.90)	0.72 (0.64–0.79)
Interval (30 day) ^c	0.16 (0.04–0.50)	0.16 (0.03–0.49)	0.05 (0.01–0.16)	0.00 (0.00–0.34)	0.00 (0.00–0.01)

^a Duckling survival using a conservative mortality estimate in which 36 ducklings were considered alive at time of radio-tag signal loss and were right-censored thereafter.

^b Duckling survival using a liberal mortality estimate in which radio-tag signal loss was considered to be entirely confounded with mortality of the duckling.

^c Daily and interval survival rates calculated while holding explanatory variables at their means.

^d Predictor levels based on 10th and 90th percentiles of each explanatory variable while holding all other variables at their mean.

experiencing signal loss as mortalities on the last day we located a signal, assuming death occurred between date of last detection and signal loss. This model included 87 mortalities and 5 ducklings that survived to 30 days post-hatch. The top ranked model for the liberal estimate of duckling survival included wetland, daily precipitation, and hatch date ($w_i = 0.48$; Table 1). Daily duckling survival was positively correlated with daily precipitation ($\beta = 0.33 \pm 0.20$) and negatively correlated with hatch date ($\beta = -0.01 \pm 0.003$). We estimated daily and interval survival rates of ducklings among wetlands with daily precipitation and hatch date held at their means (Table 2). Interval duckling survival was 0.16 (95% CI = 0.03, 0.50) for both managed impoundments and the Mandri lagoon complex, 0.05 (95% CI = 0.01, 0.16) for mangrove, and virtually zero in unmanaged impoundments and Santa Teresa lagoons (Table 2).

There were 2 competing models in the liberal analysis of duckling survival (Table 1). The first competing model ($w_i = 0.27$) included wetland and the negative influence of hatch date ($\beta = -0.01 \pm 0.003$). The next competing model ($w_i = 0.25$) included wetland and positive influences of daily precipitation ($\beta = 0.39 \pm 0.21$), duckling mass ($\beta = 0.18 \pm 0.08$), brood size ($\beta = 0.03 \pm 0.05$), and average daily distance moved ($\beta = 0.0001 \pm 0.001$), and negative influences of hatch date ($\beta = -0.01 \pm 0.004$) and female mass ($\beta = -0.007 \pm 0.005$).

Brood Survival

We calculated daily brood survival rates and 30-day interval survival for 31 broods from 2000 to 2002. Twenty-five (80.6%) of 31 females experienced total brood

loss 1–24 days post-hatch. The most parsimonious model explaining brood survival included influences of daily precipitation, hatch date, and female mass ($w_i = 0.50$; Table 1). Daily survival estimates were positively correlated with daily precipitation ($\beta = 0.78 \pm 0.52$; Figure 2A) and female mass ($\beta = 0.01 \pm 0.007$; Figure 2B), but negatively correlated with hatch date ($\beta = -0.02 \pm 0.006$; Figure 2C). Holding daily precipitation, hatch date, and female mass at their means, daily brood survival was 0.95 (0.92–0.97) giving a 30-day brood survival estimate of 0.22 (0.10–0.44). Two competing models for brood survival included subsets of the 3 variables in the best model (Table 1). One model included only female mass ($\beta = 0.01 \pm 0.007$) and hatch date ($\beta = -0.02 \pm 0.06$). The second model included daily precipitation ($\beta = 0.68 \pm 0.50$) and hatch date ($\beta = -0.01 \pm 0.006$).

DISCUSSION

The overall survival rates of ducklings and broods that we observed at Humacao were among the lowest reported for dabbling ducks, perhaps as a consequence of changes in habitats and predator communities in Puerto Rico. Inherent uncertainty in fates of 36 ducklings in our study produced great ranges in 30-day duckling survival between our conservative and liberal estimates. However, duckling survival generally corresponded with other published reports of low brood and duckling survival (Talent et al. 1983, Rotella and Ratti 1992). Even in relatively pristine environments of Alaska, 30-day survival of Northern Pintail (*A. acuta*) ducklings was low (0.04–0.14; Grand and Flint 1996). For Mallard (*A. platyrhynchos*) ducklings

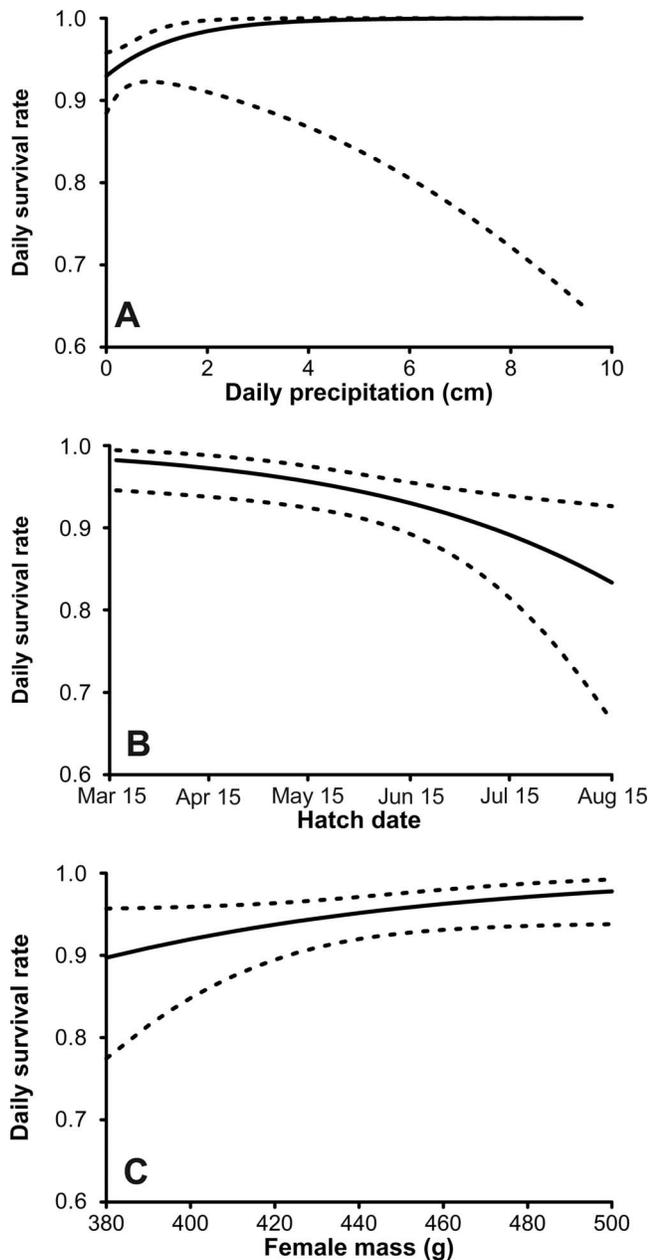


FIGURE 2. Daily survival rates (\pm 95% CI) for the most parsimonious model of White-cheeked Pintail brood ($n = 31$) survival at Humacao Nature Reserve, Puerto Rico, from 2000 to 2002. Responses are shown for each parameter in the model while holding the remaining parameters at their mean values.

in the Prairie Pothole Region, 30-day survival across site-years ranged from 0.07 to 0.34, which was among the lowest ever reported for the species (Amundson and Arnold 2011). Survival estimates in our and other studies, in both pristine and highly modified systems, demonstrate that duckling survival is generally low, but varies among species, years, and environments.

Despite the compromise in producing precise estimates of duckling survival, similar patterns of wetland-related duckling survival resulted from our conservative and liberal analyses. Wetland emerged in all competitive models in both analyses. Daily precipitation positively influenced duckling survival in both conservative and liberal analyses, but with wide confidence intervals. Survival was negatively associated with hatch date in all models in the liberal analysis, although again with broad confidence intervals.

Wetland Type and Duckling Survival

Mandri lagoon complex. Duckling 30-day survival in Mandri ranged from 0.16 (liberal) to 0.60 (conservative) and was comparable to or exceeded that for managed impoundments. Females nested in the Mandri lagoon complex in small patches or hummocks of vegetation, positioning their nests in grasses above water averaging 30 cm in depth, and then moved their broods to pond apple swamps or cattail wetlands (López-Flores 2005). We found a total of 17 nests in the Mandri lagoon complex. This complex contained the most open water and greater salinities of all Humacao wetlands, yet duckling survival tended to be higher there. This may be related to females rearing their broods primarily in Mandri III lagoon, which contained interspersed cattail and ferns, shallow water (≤ 28 cm \pm 0.01), and mudflat (Rundle et al. 2002). Unlike the Santa Teresa lagoons, mangroves were absent from the shoreline of the Mandri lagoon complex, thus providing no perches for predatory wading birds. We periodically observed females and ducklings in open waters of Mandri, but broods tended to move beneath wetland ferns, which may have shielded them from avian predators. Generally, vegetation structure and wetland habitat conditions of Mandri III lagoon were comparable to the managed impoundments. White-cheeked Pintail ducklings may have benefited from vegetation and water-level management practices implemented in the Mandri lagoon complex compared to other Humacao wetlands (Cruz-Burgos 2005). Managers emphasized interspersed herbaceous vegetation and shallow water (e.g., ≤ 30 cm) for cover and invertebrate substrates. Mandri is adjacent to managed impoundments, which probably enhanced duckling survival.

Managed impoundments. White-cheeked Pintails nested in these impoundments in 2001 ($n = 8$ nests) and 2002 ($n = 4$). Duckling 30-day survival ranged from 0.16 (liberal) to 0.46 (conservative). In fact, duckling survival may have been even higher had it not been for the total loss of one brood ≤ 2 days following draining of the impoundment (Cruz-Burgos 2005). Interspersion of herbaceous cover and shallow water, as described above for Mandri III lagoon, were likely important to duckling survival.

Mangrove forest. Survival of White-cheeked Pintail ducklings was ~ 0.01 (liberal) to 0.16 (conservative) in mangrove forest. While we never found nests in mangrove wetland, some females moved their broods there immediately after hatching (López-Flores 2005). Mangrove may harbor abundant invertebrates for foraging birds, such as fiddler crabs (*Uca* spp.; Odum et al. 1982, Smith et al. 1991, Nagelkerken et al. 2008), shallow water, and cover for broods. Mangrove forests also are favored by wading birds for roosting and nesting (Frederick 2002). The forested structure of mangroves at Humacao provided perches and shelter for potential duckling predators, such as Yellow-crowned Night-Heron (*Nyctanassa violacea*), Black-crowned Night-Heron (*Nycticorax nycticorax*), and Great Egret (*Ardea alba*; López-Flores 2005).

Unmanaged impoundments. There were 4 units that flooded either by receiving water from Santa Teresa II, rainfall, or saltwater intrusion. Thirty-day duckling survival in these impoundments was < 0.03 , and we never found nests there. Impoundments were overgrown with vegetation, often dry and unavailable to broods, or when shallowly flooded were covered by dense monotypic cattail with $< 20\%$ open water. Deeper portions of unmanaged impoundments were mostly used by female White-cheeked Pintails that had lost their broods.

Santa Teresa lagoons. The complex contained $> 50\%$ open water with cattail and some aquatic ferns rimming the lagoon edges. These lagoons are contiguous with mangrove wetlands and uplands. One unique characteristic of Santa Teresa is that this complex historically was considered important to breeding White-cheeked Pintails because of artificial nesting structures, existing there since 1989. However, duckling survival there was among the lowest of all Humacao wetlands (< 0.02 in both analyses). It is plausible that nest structures and current habitat conditions (e.g., water levels) may be creating an ecological trap for White-cheeked Pintails in the Santa Teresa lagoons (Gates and Gysel 1978, Davis et al. 2007). Water depths of 44 cm (± 0.02 , Santa Teresa I) and 65 cm (± 0.05 , Santa Teresa II) were associated with Santa Teresa, and the lagoons had limited interspersed vegetation (Rundle et al. 2002). The second unique feature of Santa Teresa lagoons is that the largest tarpon of any Humacao wetlands were in these lagoons (Rundle et al. 2002). Fish can be important duckling predators in some systems (Davis et al. 2007, 2009), although we were unable to confirm that any ducklings with transmitters were lost to fish.

The decision to install artificial nest structures in the Santa Teresa lagoons was made before any information on White-cheeked Pintail movement or survival was available. Consequently, the value of artificial nest structures at Humacao is low if few ducklings survive to recruitment. Artificial nest structures at Humacao could be especially

deleterious if they lure female White-cheeked Pintails away from other wetlands, particularly managed impoundments, where they might successfully nest and rear broods

Other Variables Influencing Survival

In our study, duckling survival increased with increasing daily precipitation across all wetlands, suggesting a benefit to White-cheeked Pintail ducklings and broods. Rainfall may maintain water depths in wetlands already containing some water. The subsequent interspersed water and vegetation may provide broods with hiding cover and access to foods amid wetland vegetation. In contrast, excessive rainfall later during the brood-rearing season (late summer) may deepen wetland water levels, which eliminates vegetative cover through its inundation, and consequently exposes ducklings to predators in more open water. This possibility could have influenced the lower duckling survival we observed later, particularly after mid-June (Figure 2). In tropical Puerto Rico, these advantages to rainfall early in the season may offset the disadvantages typical in temperate systems. In the northern prairies of North America, mortality of Mallard ducklings 0–7 days old increased during bouts of precipitation, when ducklings were most susceptible to inclement weather (Krapu et al. 2000, 2006). Rainy weather may induce duckling mortality because of lost body heat, additional need for brooding of young, increased exposure risk, and reduced feeding times (Krapu et al. 2000, 2006).

Other potentially positive influences of precipitation include temporarily reduced foraging effectiveness by avian predators, or reduced salinity during rain events. Ducklings of the tribe Anatini are sensitive to wetland salinity. For example, salinities of ≥ 12 ppt increased mortality of captive wild-strain Mottled Duck (*A. fulvigula*) (Moorman et al. 1991). White-cheeked Pintail ducklings may not have been negatively impacted by salinities in Mandri lagoon complex or other wetland units at Humacao, which rarely exceeded 10 ppt (Moorman et al. 1991). White-cheeked Pintails in the Caribbean commonly nest in offshore cays devoid of freshwater and in coastal lagoons characterized by low- to meso-haline conditions, suggesting they are physiologically adapted to use brackish-saline wetlands (Meier et al. 1989, McNair et al. 2006, Yntema et al. 2017). Regular nesting by White-cheeked Pintails in brackish wetlands of > 15 ppt needs further study for confirmation.

Hatch date was an important variable in the liberal analysis. Numerous studies of North American ducks have demonstrated a negative relation between hatch date and duckling or brood survival (Rotella and Ratti 1992, Grand and Flint 1996, Guyn and Clark 1999, Krapu et al. 2000, Hoekman et al. 2004, Amundson and Arnold 2011, Davis et al. 2016). In our study, we also documented a negative relation among these variables. In the northern prairies,

duckling survival likely decreases as wetland availability and quality wane seasonally (Eldridge and Krapu 1988, Rotella and Ratti 1992, Guyn and Clark 1999, Krapu et al. 2000). Reasons for greater survival of earlier-hatched White-cheeked Pintail ducklings in our study are not entirely clear but could be related to precipitation patterns (see above).

Brood Survival

Survival of White-cheeked Pintail broods (22%) was among the lowest reported for dabbling ducks but within the range for Mallards (18%, Mauser et al. 1994; 35%, Amundson and Arnold 2011; 48%, Talent et al. 1983). In some instances, nearly 53% of Northern Pintail and Gadwall (*A. strepera*) broods have been lost on prairie impoundments in Alberta, Canada (Duncan 1986). However, Guyn and Clark (1999) estimated Northern Pintail brood survival from 72% to 88% for broods in Kitsim, Alberta. Clearly, brood survival of dabbling ducks is variable, imposing differential effects on recruitment (Sedinger 1992).

Factors influencing survival of White-cheeked Pintail broods in our study included precipitation and hatch date, described above, and female mass. Body mass of female White-cheeked Pintails captured at Humacao ranged from 380 to 500 g, and positively influenced brood survival. Older females may be more experienced and retain greater body reserves through incubation than younger females (Krapu and Doty 1979, Duncan 1987). Heavier females may produce larger eggs and ducklings at hatching, which subsequently lead to greater duckling and brood survival (Amundson and Arnold 2011), or females with greater mass may have an advantage to provide improved quality brood care than lighter and perhaps more physiologically constrained females (Talent et al. 1983, Davis et al. 2007).

Brood size is another factor, not mutually exclusive of female mass, that potentially affects duckling survival (Davis et al. 2007). We did not find strong evidence that brood sizes at nest departure affected overall survival of White-cheeked Pintail broods at Humacao. However, amalgamation of duck broods is common in some species, which may lead to larger-than-average brood sizes (i.e. crèches; Gollop and Marshall 1954, Eadie et al. 1988). In our study, one brood had 20 ducklings that were approximately 2, 23, and 30 days old. We observed multiple instances of amalgamated broods of radio-tagged ducks. We also recorded a radio-tagged female adopting the brood of another radio-tagged female that was killed ~10 days post-hatch. Thus, interpreting effects of brood size on individual White-cheeked Pintail ducklings is complicated given the birds' crèching behavior and potential double-brooded reproduction. How crèching behavior influences duckling mortality is uncertain but is an interesting topic for future research, as these behaviors differ between Holarctic and tropical Anatini.

Conservation and Research Implications

Evaluating how the "island syndrome" (Novoslov et al. 2013) influences the life history strategies of Caribbean populations of the White-cheeked Pintail would contribute to an improved understanding of the ecology and conservation of Neotropical waterfowl. For example, comparing White-cheeked Pintail duckling and brood survival across islands with varying wetland conditions (e.g., Puerto Rico vs. St. Croix) but with a similar suite of introduced mammalian predators, with populations in the mainland Neotropics at similar latitudes (e.g., southern Yucatan), would help reconcile thresholds and benefits of oceanic isolation and wetland alteration.

Low duckling and brood survival of White-cheeked Pintail and its variation among Humacao wetlands could be constraining recruitment in this population. If duckling survival is consistently enhanced in habitats such as managed impoundments, it will require similar habitat management efforts elsewhere to potentially increase recruitment of White-cheeked Pintail (e.g., Kross et al. 2008). Attributes of these managed seasonal wetlands potentially providing enhanced duckling survival would include shallow water levels (e.g., ≤ 30 cm) precluding use by predatory fish, interspersed herbaceous vegetation and water that promotes aquatic invertebrates and facilitates brood travel through an impoundment (e.g., Murkin et al. 1997), and lack of nearby mangrove forest that may support potential predators such as night-herons.

The unmanaged impoundments at Humacao could be restored to promote suitable habitat for breeding and migratory waterfowl and other waterbirds. This system has deteriorated because sites reverted to either open water or dense vegetation. The Santa Teresa II Lagoon could serve as a reliable water source for the 3 unmanaged impoundments, which would enhance their manageability. These impoundments were constructed as part of environmental mitigation for a highway development and remain under the domain of the Puerto Rico Transportation Authority. Transferring these impoundments and the surrounding area to the Humacao Nature Reserve would allow the Puerto Rico DNER to restore habitat conditions. Expanding restoration and management to other coastal wetland areas of Puerto Rico will benefit the White-cheeked Pintail and other native waterfowl in this part of the eastern Caribbean.

The current aggregation of artificial nesting platforms in Santa Teresa lagoons may be functioning as an ecological trap for White-cheeked Pintail broods at Humacao (Van Horne 1983, Davis et al. 2007, 2009). Removing nest structures from Santa Teresa lagoons and prioritizing those lagoons for fisheries resources may reduce predation risk and loss of White-cheeked Pintail ducklings and broods produced therein. This management compromise may improve opportunities for anglers at Humacao while redirecting efforts there to enhance duckling survival in

other locations of the reserve. Lastly, development of demographic or population matrix models may be required to more fully realize the influence of duckling survival on population status in White-cheeked Pintails at Humacao.

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Author contributions: FJV, RMK, and ML-F conceived the idea, JBD, FJV, RMK, JDL, and ML-F wrote the paper, ML-F and JAC-B conducted the research, and JDL analyzed the data.

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