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Breeding biology of Wilson's Plover (*Charadrius wilsonia*) and Black-necked Stilt (*Himantopus mexicanus*) on the Guianas coast

Thomas Pagnon,^{1*} Cyril Marmoeux,^{1,2} Régis Gallais,^{1,3} and Charlotte Francesiaz⁴

ABSTRACT—Many shorebirds rely on sandy beaches to breed. However, these ecosystems are rare and unstable on the Guianas coast because of sediment dynamics. Nonetheless, they host 2 shorebirds that breed in the Nearctic and the Neotropic: Wilson's Plover (*Charadrius wilsonia*) and Black-necked Stilt (*Himantopus mexicanus*). We studied their breeding biology in the Amana Nature Reserve, a Ramsar Site in French Guiana, on sandy beaches bordered by brackish lagoons during 1 breeding season. From early June to late August 2008, we located and monitored 19 Wilson's Plover and 15 Black-necked Stilt nests. Most nests were associated with bare ground. While stilts preferred to build their nests with twigs closer to lagoons, plovers did not show any preference in nest location and composition. For plovers and stilts, clutch sizes were 2–3 eggs or 3–4 eggs per nest, respectively, and the mean egg volumes were $12.1 \pm 0.4 \text{ cm}^3$ and $20.6 \pm 0.6 \text{ cm}^3$, respectively. The apparent hatching success for both species was low, 11% for Wilson's Plover and 13% for Black-necked Stilt, whereas daily nest survival was high for both species. Clutch sizes, egg dimensions, and egg colorations were comparable to those described elsewhere, but the breeding season started later than at other localities for the Wilson's Plover. In French Guiana, the apparent nest success values for both species were much lower than those reported in the United States and the West Indies but seemed slightly higher than in Brazil. Human activity impacts were limited in our study area and did not explain the low nest success values found. Beach flooding at high tide was the main cause of clutch failure, followed by predation. Ironically, flooding allows the maintenance of this low, open, and debris-covered habitat used by beach-nesting shorebirds. Received 28 September 2022. Accepted 11 August 2023.

Key words: breeding success, French Guiana, nest survival, sandy beaches, shorebird ecology.

Biologie de la reproduction du Pluvier de Wilson (*Charadrius wilsonia*) et de l'Échasse d'Amérique (*Himantopus mexicanus*) sur la côte des Guyanes

RESUMEN (French)—Beaucoup de limicoles dépendent des plages sableuses pour se reproduire. En raison de la dynamique sédimentaire, ces plages sont rares et instables sur la côte des Guyanes. Néanmoins, elles abritent deux espèces de limicoles nichant dans le néarctique et le néotropique: le Pluvier de Wilson (*Charadrius wilsonia*) et l'Échasse d'Amérique (*Himantopus mexicanus*). Nous avons étudié la biologie de leur reproduction dans la réserve naturelle de l'Amana, un site Ramsar en Guyane Française, sur des plages sableuses bordées de lagunes saumâtres pendant une saison de reproduction. De début juin à fin août 2008, nous avons localisé et suivi 19 nids de Pluvier de Wilson et 15 nids d'Échasse d'Amérique. La plupart des nids étaient associés à des sols nus. Le pluvier de Wilson n'a montré aucune préférence quant à l'emplacement et à la composition des nids. Tandis que l'Échasse d'Amérique préférait construire son nid avec des brindilles plus près des lagunes. La taille des couvées était respectivement de 2–3 œufs et de 3–4 œufs par nid, et le volume moyen des œufs était de $12.1 \pm 0.4 \text{ cm}^3$ et $20.6 \pm 0.6 \text{ cm}^3$. Le succès apparent d'éclosion était faible pour les 2 espèces, avec 11% pour le pluvier et 13% pour l'échasse, alors que la survie journalière des nids était haute. La taille des pontes, la dimension et la coloration des œufs étaient comparables à celles décrites ailleurs, mais la période de reproduction était plus tardive chez le Pluvier de Wilson. En Guyane française, les succès apparents des nids des deux espèces étaient beaucoup plus faibles que ceux observés aux États-Unis et aux Antilles, mais ils semblaient légèrement plus élevés qu'au Brésil. Les activités humaines étaient limitées sur le site d'étude et n'ont pas expliqué ce faible succès. La submersion des plages lors des grandes marées était la principale cause de l'échec des pontes, suivie par la prédation. Mais ces submersions ont paradoxalement participées au maintien de cet habitat bas, ouvert et couvert de débris utilisé par les limicoles nichant sur les plages.

Mots clés: écologie des limicoles, Guyane française, plages de sable, succès reproducteur, survie des nids.

The 1,600 km-long Guianas coast, located between the Amazon Delta in Brazil and the Orinoco Delta in Venezuela, has an Amazon-influenced, constantly evolving shoreline composed of shifting

muddy banks and sandy cheniers. The Amazon River discharges fine sediments that are transported northwestward along the coast by marine currents in the form of fluid muddy banks that become mudflats by an inshore accumulation and then are progressively colonized by mangroves (Froidefond et al. 2004, Anthony et al. 2010). This progradation is followed by a retreat and then by the formation of sandy cheniers composed of sand and shell deposits driven by waves (Anthony and Dolique 2004, Lefebvre et al. 2004). The beaches subsequently constituted remain rare and unstable (Prost 1989) but offer a natural habitat for local

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shorebirds in the mangrove-dominated Guianas shoreline.

Those scarce sandy beaches host 2 breeding shorebirds: the Wilson's Plover (*Charadrius wilsonia*) and the Black-necked Stilt (*Himantopus mexicanus*). These birds are widely distributed in the Americas, from the United States to Brazil and Peru, including the West Indies (Hayman et al. 1986, Corbat and Bergstrom 2000, Lunardi et al. 2015) and they are year-round residents in the Neotropical region (Taylor 2005). Globally, these shorebirds are classified as Least Concern by IUCN (2017). However, Wilson's Plover and Black-necked Stilt are categorized as Critically Endangered and Endangered, respectively, by the French Guiana Red List (Moncorps et al. 2017).

In this French overseas territory on the Guianas coast, the Wilson's Plover can be observed year-round on sandy beaches, from the island of Cayenne to the Maroni River at the border with Surinam. This plover also uses rice fields for chick-rearing and rocky outcrops as a resting place at high tide (TP, pers. obs.). The Black-necked Stilt can be observed throughout the year, primarily around the northwest coast also using rice fields and some estuary lagoons. The population size of both species in French Guiana is unknown. Similarly, knowledge about their breeding biology is scarce and mostly comes from studies made in the United States and in non-Amazonian Brazil (e.g., Rodrigues et al. 1996, Sordahl 1996, Conway et al. 2005a, Hood and Dinsmore 2007, Lunardi and Macedo 2010). In French Guiana, only Tostain et al. (1992) reported rare observations of Wilson's Plover nests in its northwest coast, later followed by Delsinne et al. (2003) who described displays, incubation, rearing behavior, and territoriality for 3 nests. No breeding data are available on Black-necked Stilt and this bird was considered a hypothetical breeder on the Guiana coast.

In this paper, our aims are to describe the breeding biology, nest features, and reproductive behavior of these 2 shorebirds in French Guiana, and to assess their nesting success and potential threats.

Methods

Study area

The study was conducted in the Ramsar-designated Amana Nature Reserve (Ramsar List 2023), which

is the main known breeding site for Wilson's Plover and Black-necked Stilt in French Guiana. This protected wetland is located in the mid portion of the Guianas shoreline, in the coastal plain of lower Mana River in northwestern French Guiana, delimited to the east by the Organabo River and to the west by Maroni River bordering with Surinam (Fig. 1). The coastline is characterized by active morphosedimentary changes under the influence of the Amazon River sediment dispersion system. It results in a specific morphodynamical system with alternating areas of accumulation (mud banks colonized by mangrove) and erosion (sand cords or mangroves in decline). This environment is therefore subject to a perpetual evolution (Anthony et al. 2010). This process generates a mosaic of varied habitats: sand dunes, mud flats, coastal mangroves, estuary mangroves, brackish lagoons, freshwater marshes, flooded savannas, swampy forests, and palm forests.

Our study was carried out on a 10 km-long sandy beach between the Irakumpapi estuary and the locality called Aztec beach (05°38'N, 53°38'W). This natural environment is a sandy strip of land that separates the Atlantic Ocean from coastal lagoons. These lagoons occupy former rice fields silted by coastal dynamics and flooded by rain and large tides. They were progressively colonized by mangrove trees. The beach was subject to severe erosion and gradually diverted to the west (Kelle et al. 2007). During very high tides, the water level exceeded the height of the beach in some places, flattening the summit, and driving the sand toward the back to the lagoon. These events periodically flattened and widened the beach. This sandy habitat was partially covered by herbaceous vegetation consisting essentially of a small number of *Ipomoea pes-caprae*, *Ipomoea stolonifera*, *Canavalia maritima*, and *Vigna luteola* (Péron et al. 2013). It was also covered with numerous dead trees, pieces of bark, and tide-deposited driftwood.

Nest search

Based on breeding seasons described for Surinam (Spaans 2003), we selected a prospecting period from early June to early November to search for nests. The survey started 11 June and ended on 26 August 2008, when no new nests were found, and

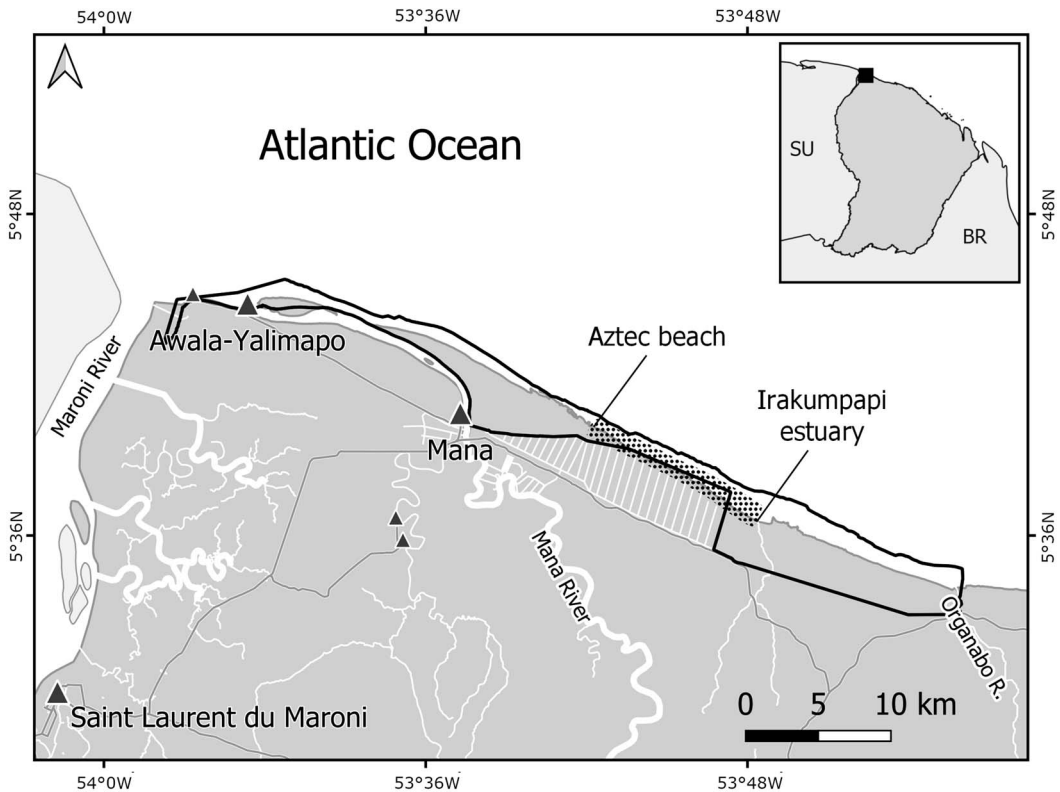


Figure 1. Nesting Black-necked Stilt and Wilson's Plover study area on the northwest coast of French Guiana. The bold black line delineates the Amana Nature Reserve. The survey site was located between Aztec beach and Irakumpapi estuary and is indicated by the area shaded with dots. Black triangles symbolize towns.

no active nests remained. We collected data during a total of 11 d of fieldwork with a weekly interval with no field activity to limit observer disturbance. We extensively explored—on foot, with binoculars—the beach and lagoon shores right down the sand cord to look for adults with nesting behavior (e.g., alarm calls, wounded bird simulations) and then located nests by following birds until they returned to the nest and resumed incubation. We identified and noted the GPS location of each nest. Nests were marked with 50 cm-tall wooden stakes placed 5 m from the nest to enable faster observer localization and avoid nest predation by reducing disturbance during our monitoring (Bergstrom 1988).

Nest description and monitoring

For each nest, we described and measured habitat features (vegetation density, ground slope, and presence of dead wood), nest location, and

surroundings (distance from the backshore brackish lagoon, distance from the sea at high tide with average tidal coefficient), and nest characteristics (construction material and external diameter). Vegetation density was expressed as the ground cover percentage with 4 categories (barren soil, <25%, 25–50%, and >50% ground cover). When eggs were found, we measured their length and width using calipers, and lightly numbered each egg with a pencil for long-term identification (Bomford 1988). The laying date was determined either by the first-laid eggs, when the clutch was found incomplete (<3 eggs), or by backdating eggs when the hatching date was recorded. We assumed that the egg-laying period would be 4 d for a 4-egg clutch and that incubation would start the day before clutch completion. Incubation is known to last 24 d for Black-necked Stilt (Sordahl 1996) and 25 d for Wilson's Plover (Bergstrom 1988).

Clutch size was considered complete when no additional eggs were observed during a follow-up nest visit. Once located, each nest was monitored weekly until its fate was recorded, as recommended by Paton (1995) and Rebergen et al. (1998). For each visit, we first made a 2 min stop about 15 m away from the nest to record parental behavior (e.g., presence on or around the nest, alarm call due to our presence). After that, we surveyed the nest (around 2 min per nest, to minimize the time when eggs were unattended). We also recorded the presence of disruptive elements (e.g., dogs, humans, turtles), number of eggs, and nest status (active, abandoned, or egg loss) during each survey. Since shorebird chicks are precocial and leave the nest in the hours following hatching, empty nests around the theoretical hatching date were considered successful only when we found clean, small shell fragments or half shells (Page et al. 1985). When we found nests that were totally empty, without evidence of hatching, or with cold or damaged eggs, we considered such nests as failed. In those cases, we attempted to identify possible causes by examining nest condition (destroyed or washed), the condition of the eggs, and potential clues around nest sites (eggshells, animal tracks, or footprints). The causes of failure were recorded as predation (e.g., by dogs, birds, or iguanas), flooding, desertion, or destruction (by turtles or humans). The disappearance of eggs without any trace was classified as “undetermined outcome.”

Data analyses

We tested for differences in the choice of nest construction material and the clutch size with a 2-proportion *z*-test with Yates’s continuity correction or chi-square goodness of fit test, depending on the number of observations (degrees of freedom). We tested for potential significant differences of nest position with respect to sea and lagoons with Wilcoxon signed-rank test. Mean values are expressed with standard deviation. *P* values < 0.05 are considered statistically significant. All statistical analyses were conducted in program R 4.2 (R Core Team 2022).

We calculated egg volume using the Hoyt (1979) method, whose formula is $V = 0.467 LW^2$ for Black-necked Stilt and $V = 0.476 LW^2$ for Wilson’s

Plover (based on Dunlin [*Calidris alpina*] coefficient), where *L* is length and *W* is width. Reproductive success was determined through the apparent hatching success (i.e., percentage of nests with at least 1 hatched egg). Predation rate was defined as the percentage of preyed upon egg-stage nests (Rebergen et al. 1998). Nest survival was calculated using the Mayfield (1975) method, which includes the duration of exposure of nests to predation, parasitism, poor weather conditions, etc. This survival is expressed in daily survival probability (i.e., the probability that a nest will survive from one day to the next), and in nest survival (i.e., the probability that a nest fledges at least 1 young).

The Mayfield equations are:

Daily survival probability

$$= 1 - \frac{\text{Total number of failed nests}}{\text{Total number of exposure days}}$$

Nest survival

$$= \text{Daily survival probability}^{\text{Nesting period}}$$

Results

Breeding phenology

During our study period, we found 19 Wilson’s Plover and 15 Black-necked Stilt nests. On the first survey day, on 11 June 2008, 6 nests already contained eggs. The first stilt chick hatched on 20 June, and the first plover on 24 June. The laying dates were estimated to be 27 and 30 May, respectively. The last active nests were found on 1 July for Black-necked Stilt and on 23 July for Wilson’s Plover. They may be renesting or clutch replacements, but we had no evidence of it. Although all plover nests were empty at the end of July, a new nest with a single cold egg was discovered on 7 August. One week later, this unique egg was still cold. We assumed that it was a late abandoned replacement clutch. As the nest was not active anymore upon observer discovery, we did not take it into account in breeding success analyses.

Nest characteristics

The Wilson’s Plover builds its nest on beaches with < 15% slope. Nests are not evenly distributed

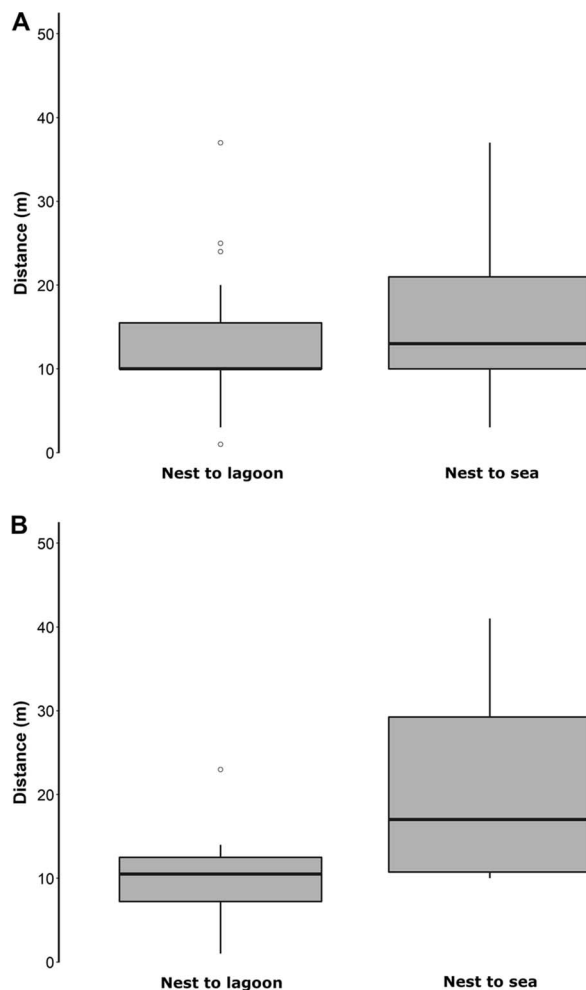


Figure 2. Mean (\pm SD) distances to sea at high tide with an average tidal coefficient and backshore brackish lagoon of Wilson's Plover nests (A) and Black-necked Stilt nests (B) in Amana Nature Reserve, French Guiana.

and distances among them vary. We noticed that some were located close to stilt nests. We found that plovers preferred to nest in areas without vegetation cover (79%, $n = 15$) rather than areas dotted with few small patches of plants (21%, $n = 4$; $\chi^2 = 10.526$, $df = 1$, $P < 0.001$). Plovers build their nest at a similar distance between the coast and the lagoon ($V = 62.5$, $P = 0.32$; Fig. 2). They are mostly set leaning against dead wood (29.4%) or between 2 pieces of wood (58.8%), and sometimes close to a rock (Supplemental Fig. S1). We found a nest within a *Montrichardia arborescens*, a perennial shrub commonly found along riverbanks, whose dry stem was folded into a diamond shape.

The nests consisted of a shallow depression scraped in the sand with a diameter of 10–12 cm (95% CI). They were lined with either a few wood twigs (42%, $n = 8$), shells (10%, $n = 2$), or a mix of twigs and shells (32%, $n = 6$), and sometimes supplemented with small pebbles (16%, $n = 3$). Wilson's Plover did not have a particular preference for the nest composition ($\chi^2 = 4.7895$, $df = 3$, $P = 0.18$), and the quantities of each component varied greatly from one nest to another (Table 1).

Black-necked Stilt used the same sandy nesting habitat as Wilson's Plover. Their nests were more frequently located in areas without vegetation or with low scattered plants than in densely vegetated

Table 1. Wilson's Plover and Black-necked Stilt nest compositions in French Guiana's Amana Nature Reserve sandy beaches. All values are expressed as a percentage.

	Twigs	Shells	Stones	Twigs and shells	Shells and stones	Twigs, shells, and stones
Wilson's Plover	42	10	0	32	0	16
Black-necked Stilt	67	0	0	13	7	13

areas covered with *Ipomea* sp. vines ($\chi^2 = 19.2$, $df = 1$, $P < 0.001$), but we found no significant difference between barren (60%, $n = 9$) and vegetated habitats (40%, $n = 6$; $\chi^2 = 0.5333$, $df = 1$, $P = 0.46$). Stilts chose locations closer to the lagoon than to the sea ($V = 6$, $P = 0.003$; Fig. 2). It seems that most stilts bred in small colonies composed of 4 nests on average, but we did not collect enough data to quantify this. Nests are scrapes systematically arranged with an assembly of small wood twigs (Supplemental Fig. S2) and their diameters ranged from 19 to 24 cm (95% CI). Other materials are sometimes used besides twigs, such as pebbles (7%, $n = 1$), shells (13%, $n = 2$), or a mix of both (13%, $n = 2$). The majority of nests contained only twigs (67%, $n = 10$) but this preference is not statistically significant ($\chi^2 = 2.1333$, $df = 1$, $P = 0.14$; Table 1).

The nests of these 2 shorebirds were located close to those of other species. We found Common Ground Dove (*Columbina passerina*) nests and an unidentified, but most likely Lesser Nighthawk (*Chordeiles acutipennis*), nest on our study site.

Clutch size and egg biometry

The clutch size in Wilson's Plover was 2–3 eggs per nest (95% CI, $n = 18$). Clutches with 3 eggs

were the most frequent (13 nests), accounting for 72% of the total eggs, but these clutches were not significantly predominant ($\chi^2 = 1.6842$, $df = 1$, $P = 0.19$). The length and width of the 47 eggs measured were 35.3 ± 0.4 mm and 26.8 ± 0.4 mm, respectively. Egg volume ranged between 9.7 and 16.6 cm^3 , with a mean volume of $12.1 \pm 0.4 \text{ cm}^3$.

With a clutch size of 3–4 eggs per nest (95% CI, $n = 15$), the Black-necked Stilt generally laid 4 eggs ($\chi^2 = 4.2667$, $df = 1$, $P = 0.039$). Stilt eggs were subelliptic to oval in shape, smooth, and slightly glossy, greenish with black and gray stains. We measured 48 eggs laid by 15 different females. Their mean length was 43.4 ± 0.5 mm and their mean width was 31.8 ± 0.4 mm, which is a mean volume of $20.6 \pm 0.6 \text{ cm}^3$ (range: 17.2–25.9 cm^3 ; Table 2).

Parents' behavior

In only 8% of visits by Wilson's Plover, we observed 1 of the adults incubating on the nest. It seems that they noticed potential danger from afar and quickly ran away and tried to hide when they were about 20 m from the observer. This behavior was discreet and fast, which is why it has rarely been observed. Moreover, when an observer moved away from the nest, one could see it

Table 2. Eggs and clutch sizes of Wilson's Plover and Black-necked Stilt nesting on sandy beaches in French Guiana's Amana Nature Reserve. Numbers in parentheses correspond to n .

	Wilson's Plover	Black-necked Stilt
Number of eggs	47	52
Length (mm)	35.3 ± 0.4 (47)	43.4 ± 0.5 (48)
Width (mm)	26.8 ± 0.4 (47)	31.8 ± 0.4 (48)
Volume (cm^3)	12.1 ± 0.4 (47)	20.6 ± 0.6 (48)
Number of clutches with 1 egg	2	1
Number of clutches with 2 eggs	3	2
Number of clutches with 3 eggs	13	1
Number of clutches with 4 eggs	0	11

Table 3. Nest fates, hatching successes, and nest survivals for Wilson's Plover and Black-necked Stilt nesting on sandy beaches in Amana Nature Reserve, French Guiana. All values are expressed as percentages.

	Wilson's Plover	Black-necked Stilt
Successful nest	11.1	13.3
Depredated nest	7.7	13.3
Flooded nest	33.3	20
Destroyed nest	5.5	0
Abandoned nest	0	0
Unknown fate	22.2	53.3
Apparent hatching success	11	13
Daily nest survival probability	93.6	95.8
Nest survival probability	12	25.3

returning after a while. During our observation sessions, parents stayed close and responded as alarmed when attending active nests in 56% of cases, and 18% when unoccupied. Generally, adults mimicked a breeding site elsewhere when attending nests and more rarely mimicked a broken wing to divert attention.

Nesting Black-necked Stilts seem to use the same responses to intruders as Wilson's Plovers. Only 1 female was seen brooding. In all other cases, parents had already left the nest when we started our observations. Unlike plovers, stilts do not run away, but take off from a distance to prevent the nest from being found. However, when we were making observations close to active nests, one or both parents came back and signaled alarm in around 68% of the cases. This behavior is also noted when the nest was empty in 27% of our visits.

Hatching success and nest failure

Only 2 out of 18 Wilson's Plover clutches (11%) hatched. Despite a 93% probability of daily nest survival, total nest survival did not exceed 12%. Such high failure rate is mostly due to predation from diverse sources (28%) and beach flooding during very high tides (33%). Accidental destruction by sea turtles remained negligible.

Despite the fact that an important part of nests recorded had an unknown outcome, nest survival reached 25% for Black-necked Stilt. The probability that at least 1 chick fledged was relatively low given the small number of nests found. However, daily survival was high with a 95% chance that the nest would survive from one day to the next. Predation

and nest submersion related to shoreline erosion accounted for 13% and 20% of nest fates, respectively (Table 3).

Discussion

Our study is the first description of the breeding biology of 2 Nearctic–Neotropical shorebirds living on the Guianas coast in South America. It provides nesting characteristics that we can compare to the ones observed in different biogeographic areas. Wilson's Plovers nest on sandy beaches bordered by brackish lagoons or mangroves. They bred from May to July in French Guiana, which corresponds to the long rainy season. The same phenology has been observed in Surinam, the neighboring country (Spaans 2003). However, the breeding season lasts longer in northeastern Brazil, from Maranhao to Bahia, with nests found between April and October (Rodrigues *et al.* 1996, Lunardi and Macedo 2010, Andrade *et al.* 2020). In the Lesser Antilles and the United States, the breeding season starts earlier, in March–April (Smith and Smith 1999, Levesque *et al.* 2005, Brown and Brindock 2011, Brown and Snyder 2013) and in April (Bergstrom 1988, Corbat 1990, Stevenson and Anderson 1994, Corbat and Bergstrom 2000), respectively.

Plover eggs were similar in number, size, and coloration to those of clutches described previously for this bird (Rodrigues *et al.* 1996, Lunardi and Macedo 2010, Zdravkovic *et al.* 2018, Andrade *et al.* 2020). Their nests consisted of depressions scraped in the sand, always hidden by surrounding stones, driftwood, or other beach debris. Bergstrom (1988) suggested that they act

as a shield to protect the nest against the wind. Such barriers would prevent the eggs from rolling out of the nest. On our study beach, with abundant natural beach debris, nests were more cryptic and probably harder to locate by predators. Page et al. (1985) felt that beach debris increases adult movement discreetness between nests and feeding sites. Hence, the high daily survival rate of Wilson's Plover nests appears to be mainly related to the spatial distribution of the various objects around the nest. Conversely, vegetation did not seem to play a role in nest protection and visibility seemed more advantageous than concealment. All nests found were carefully placed in an area that contained bare ground away from the vegetation or, more rarely, in the middle of a few scattered clumps of plants. Dense vegetation could hinder early visual detection of predators, prevent nest escape when approached by a predator, and provide hiding places for potential predators (Gotmark et al. 1995, Hood and Dinsmore 2007).

Wilson's Plovers have a limited ability to defend their own nests (Ruiz-Guerra et al. 2008). Like most shorebirds, they developed adaptations such as cryptic coloring of adults, eggs, and chicks, discreet nest escape behaviors, extreme mobility, and nidifugous behavior in juveniles (Page et al. 1983). Nests close to other nests, however, may influence individual chances of success and that of their neighbors. Indeed, the nests we studied were >100 m from each other. However, their relative proximity to those of Black-necked Stilts seems to indirectly benefit plovers due to stilt surveillance and protection, thereby increasing their chance of survival (Quinn and Ueta 2008). Such protective nesting association has already been observed, for example, with Red-billed Coughs (*Phyrrhonorax phyrrhonorax*) nesting near Lesser Kestrel (*Falco naumanni*) colonies (Blanco and Tella 1997), and White-tufted (*Rollandia rolland*) and Silvery (*Podiceps occipitalis*) grebes near Brown-hooded Gull (*Chroicocephalus maculipennis*) colonies (Burger 1984), who benefit from their associated species' defense behaviors.

The Black-necked Stilts nested on sandy beaches on the edge of lagoons between May and July in French Guiana. However, some active nests and chicks were observed between September and

November on rice fields (Groupe d'Etude et de Protection des Oiseaux en Guyane, 2022, unpubl. data). A second nesting period seems to occur farther inland. In Surinam, where habitats and climate are very similar to French Guiana, Spaans (2003) indicated that there were 2 nesting activity peaks per year in 2 different habitats: a first one close to coastal lagoons during the long rainy season (from mid-April to mid-July) and a second one in inland marshes during the dry season (from August to late November). This bimodal breeding season could be related to water levels in different habitats, with coastal lagoons too dry for nesting during the dry season and marsh water levels too deep during the rainy season.

Some avian species show substantial variations in life-history traits along latitudinal gradients (Martin et al. 2000, Cardillo 2002). Although Black-necked Stilts have a large latitudinal breeding range, their breeding periods, clutch sizes, and egg dimensions in French Guiana resembled those described for populations in United States and Brazil (Sordahl 1996, Conway et al. 2005b, Ackerman et al. 2014, Lunardi et al. 2015, Mendonça et al. 2019). Nesting habitat and nest features seem to differ. Here, stilts selected nesting sites close to lagoons presumably because of food preference. In Puerto Rico, stilts feed on corixids in lagoons (Cullen 1994). We did not investigate invertebrates in backshore lagoons, but we assume that they could be one of the main food items for stilts. The quantity and distance to prey source may therefore influence nest success by affecting feeding efficiency and energy resources of brooding adults (Smith et al. 2007).

The nest distribution pattern of stilts seems to indicate a loose form of coloniality. According to Smith et al. (2007), the nest distribution pattern affects breeding success through density-dependent predation. A colonial strategy could induce collective defense and minimize the impact of predation (Arroyo et al. 2001). Although mobbing is common antipredator behavior in stilts (Sordahl 1990), we rarely observed such behavior. Colonial nesting could be more related to nesting habitat distribution.

The apparent nest success of both species in French Guiana was much lower than what has been reported in the United States (Bergstrom

1988, Corbat 1990, Sordahl 1996) and the West Indies (Brown and Brindock 2011). In contrast, those estimated nest success values seemed slightly higher than those of Brazil (Mendonça et al. 2019). However, a substantial proportion of nests with unknown fate may have biased our results.

Our study took place on a relatively isolated beach within a protected area. We found no direct or indirect evidence of nest destruction by humans, even though we observed people, all-terrain vehicles, and stray dogs while in the field. Predation, however, was a common cause of nest loss. Potential predators could be Atlantic ghost crabs (*Ocypode quadrata*), green iguanas (*Iguana iguana*), Yellow-headed Caracaras (*Milvago chimachima*), Black Vultures (*Coragyps atratus*), and common opossums (*Didelphis marsupialis*).

Flooding during very high tides was another major cause of nest failure. Birds breeding on intertidal habitats are generally well adapted to the risk of nest flooding by daily and semi-lunar tides, but these adaptations do not seem to prevent losses caused by stochastic extreme weather events (van de Pol et al. 2010, Bailey et al. 2017, Plaschke et al. 2019). When we conducted our surveys, the beach started a significant erosion phase with its height and width shrinking dramatically. The beach's flat surface limited the availability of safe places for nesting and nest survival might be better during sand accumulation phases. However, frequent overwashing events also generate natural erosion and sediment deposition that create and maintain this low, open, and debris-covered habitat used by beach-nesting shorebirds (DeRose-Wilson et al. 2013). To date, the coast is still facing erosion resulting in beach fragmentation, and an overall reduced expanse of suitable habitat. In a survey conducted in 2017, no nests were found, although some adults and a few chicks were observed (Groupe d'Etude et de Protection des Oiseaux en Guyane, 2022, unpubl. data). As the Guianas coast is in perpetual evolution, further research would be crucial to understand the dynamics of this nesting habitat.

The nesting population size of these 2 species of shorebirds in French Guiana remains largely unknown, like elsewhere along the Guianas coast. No global census has been carried out so far

because most of the beaches are remote and difficult to reach. Besides those known for the Amana Nature Reserve and adjacent rice fields, local ornithologists reported only 2 breeding pairs of Wilson's Plover near the cities of Kourou and Cayenne (Groupe d'Etude et de Protection des Oiseaux en Guyane, 2022, unpubl. data). Both species seem uncommon and patchily distributed, with large variations over time directly linked to coastal sedimentary dynamics. More investigations will be necessary to assess populations sizes and determine their distributions.

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