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NEST MOVEMENT BY PIPING PLOVERS IN RESPONSE TO CHANGING HABITAT CONDITIONS

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Abstract. Birds that nest along reservoir or river shorelines may face fluctuating water levels that threaten nest survival. On Lake Sakakawea of the upper Missouri River, 37 and 70% of Piping Plover (*Charadrius melodus*) nests found in 2007 and 2008, respectively, were initiated at elevations inundated prior to projected hatch date. We describe eight events at seven nests in which adult Piping Plovers appeared to have moved active nests threatened by rising water or gathered eggs apparently displaced by rising water on Lake Sakakawea and the Garrison reach of the upper Missouri River. Additionally, we describe one nest that was moved after the habitat at the nest site had been disturbed by domestic cattle. Our observations and evidence indicate that adult Piping Plovers are capable of moving eggs and establishing nests at new sites during incubation. Furthermore, our results suggest that Piping Plovers evaluate their reproductive investment under potential threat of nest loss and may be capable of acting prospectively (moving nests prior to inundation) and reactively (regathering eggs after inundation) to avoid nest failure.

Key words: Charadrius melodus, *egg movement, nest flooding, nest-site selection, nest survival, Piping Plover, prospective action.*

Desplazamiento de los Nidos de *Charadrius melodus* en Respuesta a Condiciones Cambiantes del Hábitat

Resumen. Las aves que anidan a lo largo de las costas de embalses y ríos pueden enfrentar niveles fluctuantes de agua que amenazan la supervivencia de sus nidos. En el Lago Sakakawea, parte alta del Río Missouri, el 37 y 70% de los nidos de *Charadrius melodus* encontrados en 2007 y 2008, respectivamente, fueron iniciados a elevaciones que resultaron inundadas antes de la fecha proyectada de eclosión. Describimos ocho eventos en siete nidos en los cuales los adultos de *C. melodus* parecen haber movido los nidos activos amenazados por el ascenso del agua o reunido huevos aparentemente desplazados por el ascenso del agua en el Lago Sakakawea y en el ensanche Garrison, de la parte alta del Río Missouri. Además, describimos un nido que fue desplazado luego de que el hábitat en el sitio de anidación fuera perturbado por ganado doméstico. Nuestras observaciones y evidencia indican que los adultos de *C. melodus* son capaces de mover los huevos y de establecer los nidos en nuevos sitios durante la incubación. Más aún, nuestros resultados sugieren que *C. melodus* evalúa sus inversiones reproductivas bajo la amenaza potencial de pérdida del nido y puede ser capaz de actuar de modo prospectivo (desplazando los nidos antes de la inundación) y reactivo (juntando los huevos nuevamente tras la inundación) para evitar el fracaso de sus nidos.

Birds that nest along the shorelines of reservoirs and flowing rivers may face fluctuating water levels that jeopardize nest survival. Water levels on the upper Missouri River can fluctuate markedly during the breeding season (U.S. Army Corps of Engineers 2008). Nest loss from flooding has been identified as a major factor influencing productivity of the federally listed Piping Plover (*Charadrius melodus*; U.S. Fish and Wildlife Service 1985, Burger 1987, Prellwitz et al. 1995, Espie et al. 1998). In 2007 and 2008, 37 and 70% ($n = 41$ and 60), respectively, of Piping Plover nests monitored at Lake Sakakawea, a large reservoir on the upper Missouri River, were initiated at an elevation that

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would become inundated before their projected hatch date (MJA, unpubl. data).

Piping Plovers generally select nesting sites on shorelines and sandbars that are largely devoid of vegetation, with sandy substrate broken up by larger sediments and sometimes small patches of short vegetation; often large items such as cobbles, pieces of wood, or other debris are immediately adjacent to the nest, apparently to conceal the nest and/or the incubating adult (Cairns 1982, Burger 1987, Prindiville Gaines and Ryan 1988, Espie et al. 1996; TLS and MJA, unpubl. data). The nest cup is formed by the adult as a depression in the substrate and is typically lined with small, thin, light-colored pebbles 2–10 mm in diameter (Cairns 1982, Elliott-Smith and Haig 2004). A clutch of four eggs is common for the first nesting attempt; replacement nests may include one to three eggs. Generally, eggs are laid one to two days apart and hatch after 28 days of incubation (Prindiville Gaines and Ryan 1988, Elliott-Smith and Haig 2004).

In 2007, we documented five events at four nests where adult Piping Plovers appeared to have moved their eggs, seemingly in response to changing habitat conditions within 5 m of the nest, and in 2008, we documented similar events at four nests. We describe each moved nest and discuss evidence consistent with movement of eggs by adult Piping Plovers apparently in response to changing habitat conditions.

METHODS

STUDY AREA

We made our observations during a study of Piping Plover productivity along the upper Missouri River in North Dakota between Garrison Dam and Bismarck (hereafter, the Garrison reach) and at Lake Sakakawea, a main-stem reservoir upstream of Garrison Dam. We used a stratified-random-sampling design based on historic nest densities of the Piping Plover and Interior Least Tern (*Sternula antillarum athalassos*) (U.S. Army Corps of Engineers, unpubl. data) to select 17 6.4-km and 30 2-km segments for productivity and habitat sampling at the Garrison reach and Lake Sakakawea, respectively. Landform differences between flowing river and reservoir habitats required slightly different sampling designs.

NEST MONITORING

We systematically searched study segments for nests every two to three days throughout the nesting season (April–July) in 2007 and 2008. Upon discovering a nest, we recorded a GPS location at the nest (post-processed differential correction; Trimble model GeoXT, Trimble Navigation Limited, Sunnyvale, CA; use of trade names does not imply government endorsement) and floated eggs to determine incubation stage (Hays and LeCroy 1971). Nests were photographed with a digital camera, and habitat characteristics were measured (see Sherfy et al. 2009) at nest discovery, when possible, or on a subsequent visit. Each nest was revisited three times per week, and eggs were refloated when necessary to re-evaluate incubation stage; otherwise, incubation stage was calculated from previous data. We considered a nest to be at risk of flooding if the observer believed that the previous pattern of water-level change likely would cause inundation of the nest prior to the next visit. At Lake Sakakawea, we measured the elevation of each nest relative to a benchmark, with a rotating laser level (LaserMark LMH-GR, CST/berger, Watseka, IL); benchmark elevations were subsequently measured by survey-grade GPS equipment (Trimble model 5800 and 5700, Trimble Navigation Limited). Chicks were banded shortly after hatching with unique color combinations and resighted every two to three days until they reached the age of fledging. Piping Plover productivity was monitored separately by US Army Corps of Engineers (COE) field crews.

FIGURE 1. Example of digital photographs of individual Piping Plover eggs used to identify unique patterns of egg spots for nests that were moved by adults: (A) at initial nest site; (B) at subsequent nest site.

EGG-SPOT EVIDENCE

Piping Plover eggs are cryptically colored with unique patterns of small black, brown, and purple spots on a buff background. Within a clutch eggshell spots are of similar density and size (Cairns 1982) but also vary from egg to egg (Gosler et al. 2000, Nguyen et al. 2007). Therefore, we examined unique egg-marking patterns in photographs to confirm that the egg(s) at two nest locations were the same (Fig. 1). We used six independent observers to verify the identity of individual eggs at both nest locations, and each match was confirmed by all observers.

TABLE 1. Case histories of nest movements by Piping Plovers on the upper Missouri River, including date, incubation stage, clutch size (from a subset of visits before and after the observed movement), estimated distance between nest sites, and number of eggs identified (EID) at both nest sites by photo analysis.

	Before			After				
Nest	Date	Incubation stage (days)	Clutch size	Date	Incubation stage (days)	Clutch size	Distance (m)	EID
1	18 May 2007	10	4	23 May 2007	15	3	4	1
2	9 June 2007	13	4	11 June 2007	15	4	0.6	—[a]
	14 June 2007	18	3	16 June 2007	20	3	—[b]	—[a]
3	15 June 2007	9	3	19 June 2007	13	3	4.7	2
4	30 June 2007	13	4	2 July 2007	16	4	0.3	1
5	13 June 2008	21	3[c]	15 June 2008	21	4	—[b]	—[a]
6	10 June 2008	17	4	13 June 2008	20	4	—[b]	1
7	13 June 2008	25	4	15 June 2008	27	3	—[b]	2
8	10 June 2008	18	3	13 June 2008	21	3	—[b]	—[a]

[a] Photographs of nest before and after the move were not available for examination.
[b] Distance nest moved not measured because prior location inundated.
[c] One additional egg, of unknown origin, was 2.5 m from nest prior to movement.

RESULTS

We documented nine events at eight nests (Table 1) consistent with movement of eggs by adult Piping Plovers. In five of the nine cases we used photo analysis of egg spots to confirm that at least one egg in each nest was the same (Table 1).

Nest 1. On 5 May 2007, we found a three-egg nest at the Garrison reach. On 18 May, we observed that a COE crew had installed a 1-m^2 predator exclosure (Rimmer and Deblinger 1990) around the nest. On 23 May, the eggs were missing from the original nest cup, which we determined likely was inundated following recent rain and concomitant rise in river level. On that same visit, however, we discovered three eggs in a nest cup lined with pebbles ~4 m from the previous nest site and away from the nearest shoreline (Table 1). The predator exclosure remained at the previous nest site until 27 May; on 28 May, we observed the exclosure had been moved to the new nest site. The first egg hatched on 4 June, and all three chicks survived to fledge, on the basis of observations of unique color bands applied at hatching.

Nest 2. On 30 May 2007, at Lake Sakakawea, we found a nest with four eggs that we estimated had been incubated for three days. We revisited the nest four times between the date of discovery and 9 June and observed normal nest conditions (Table 1). On 11 June, the lake level had risen, bringing the shoreline within 0.3 m of the original, but empty, nest cup. On the same visit, however, we found a four-egg nest within a cup lacking pebbles 0.6 m away, upslope from the original nest site (Table 1). Only one pair of adults was observed in the area during the time this nest was active. On 14 June, the lake level had risen and the shoreline was within 0.2 m of the second nest cup, which was now lined with pebbles and contained only three eggs (Table 1). On 16 June, the original nest cup was inundated and we found three eggs farther upslope from the shoreline than the second nest cup; they were grouped together but not set in an obvious scrape or nest cup. The final nest site was inundated on 18 June.

Nest 3. On 5 June 2007, we found a two-egg nest at Lake Sakakawea. On 15 June, the nest (Table 1) appeared to be at risk of flooding because it was 0.6 m in elevation above the water line and the shoreline was subject to frequent waves. On 19 June, the lake had risen 0.3 m (U.S. Army Corps of Engineers 2008), the original nest cup was empty, and we found a new nest 4.7 m away, upslope from the original site, that consisted of two eggs in the nest cup and one egg <1 m away (Table 1). On 21 June, a COE crew moved these three eggs and the substrate, including a pebble lining, from their current position an estimated 1 m to a third site (Fig. 2; C. J. Huber, COE, pers. comm.). On 24 June, the nest at the COE-selected site was 3.6 m away from the second site, reflecting an estimated 2.6-m discrepancy in nest locations. On 4 July, the final nest site had wave-washed substrate, eggs were missing, and no adults or unmarked chicks were found.

Nest 4. We found a nest with three eggs at Lake Sakakawea on 17 June 2007. We revisited the nest six times between 17 June and 30 June and observed normal nest conditions. Between 30 June and 2 July, one or more cattle moved through the area and left a hoof print ~5 cm deep and 0.3 m away from the nest; however, there was a small ridge between the nest cup and the hoof depression. On 2 July, the original nest cup was empty except for the pebble lining, and we found four eggs in the unlined hoof depression (Table 1; Fig. 3). Small pebbles lined the hoof depression on 4 July, and the original nest cup lacked pebbles (Fig. 3). All four eggs later hatched, and one uniquely color-banded chick was observed as a fledgling.

Nest 5. On 20 May 2008, we found a single-egg nest at Lake Sakakawea. During our sixth return visit on 2 June, we found a single egg 2.5 m away from a three-egg nest. On our tenth return visit (13 June), the original nest site had been recently inundated and the eggs were washed up along the shoreline (Table 1). On 15 June, an adult Piping Plover was incubating four eggs (Table 1) in a newly created nest cup partially lined with pebbles and located upslope from the original site. On 17 June, the second nest site was inundated and the eggs were scattered and floating in the water.

Nest 6. On 25 May 2008, we found a three-egg nest at Lake Sakakawea and subsequently observed this nest with four eggs at an estimated two days of incubation on 27 May. We observed normal nest conditions during eight subsequent visits. On 13 June, an adult Piping Plover was incubating four eggs (Table 1) at a new site upslope from the original site, which appeared to have been recently inundated, as indicated by wave-washed substrate

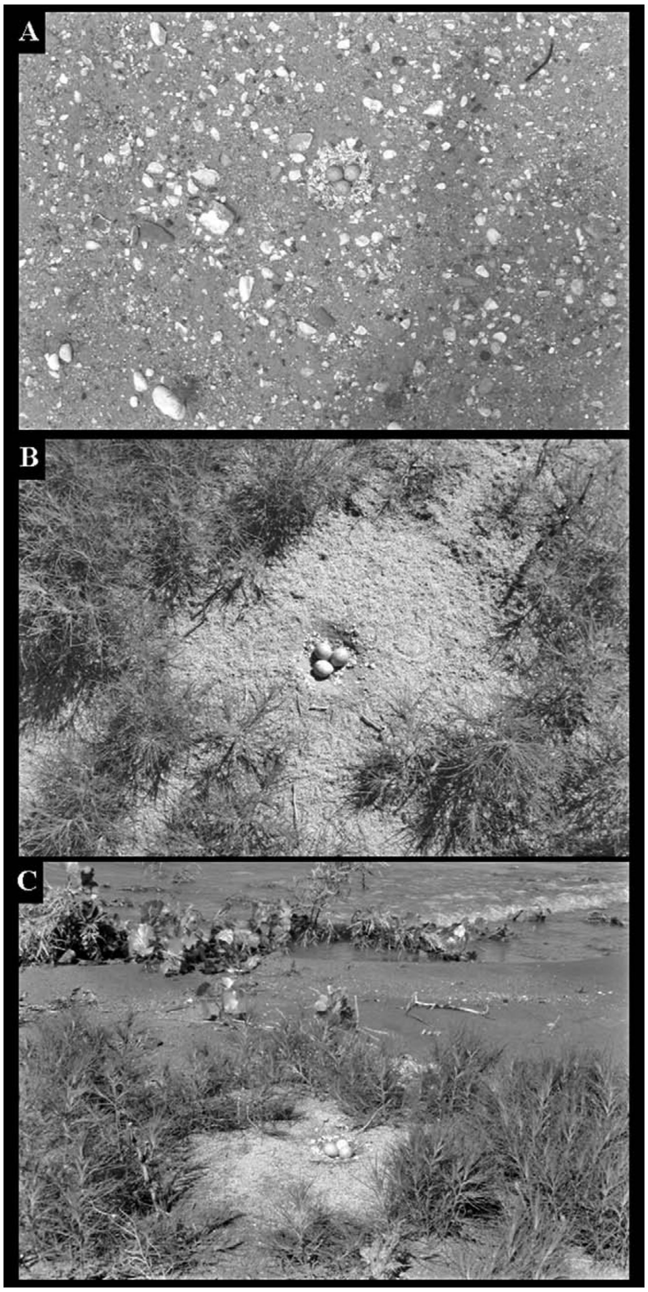

FIGURE 2. Photographs documenting a difference in nest-site habitat between two sites of the same Piping Plover nest that was threatened by rising waters at Lake Sakakawea: (A) initial nest site during low water; (B and C) final nest site.

and the presence of wrack. On 15 June, the second nest site was under water and all eggs were missing.

Nest 7. On 29 May 2008, at Lake Sakakawea, we found a four-egg nest an estimated nine days into incubation . During our eighth return visit on 15 June we observed an adult Piping Plover incubating three eggs (Table 1) in a location different from the original nest site. The new site was upslope of the original site and also appeared to have been recently inundated, as evident by wave-washed substrate and the presence of wrack. On 17 June, the second nest site was inundated, but all three eggs were in the cup and pipping. On 19 June, the second nest site was underwater, all eggs were missing, and no unmarked chicks were observed in the area.

Nest 8. On 31 May 2008, we found at Lake Sakakawea a four-egg nest at an estimated eight days of incubation. On our sixth return visit on 13 June, the original nest site was inundated and an adult Piping Plover was incubating three eggs (Table 1) at a new site upslope of the original site. The new location also appeared to have been recently inundated, as evident by wave-washed substrate and the presence of wrack. On 15 and 17 June, the three eggs were inundated, but an adult Piping Plover was nearby. On 19 June, the second nest site was underwater and all eggs were missing.

DISCUSSION

Our observations are consistent with movement of eggs by adult Piping Plovers in response to changing habitat conditions. Explanations for these observations include an attempt to renest at the new site(s) following failure of the initial nest or discovery of a previously undetected nest coincident with failure of the initial nest. Several lines of evidence suggest that neither of these alternatives applies. First, the estimated incubation stage of eggs in each new nest cup (nests 1–4) was consistent with the incubation stage expected from eggs in the original nest cup. Second, examination of egg spots in photographs of the nests at the original and new locations revealed identical patterns for one (nests 1, 4, and 6) or two (nests 3 and 7) eggs. Third, we found >95% of nests at ≤10 days incubation (MJA and TLS, unpubl. data), whereas the movements occurred at nests with eggs at >10 days of incubation. Fourth, our observations of eggs in unlined nest cups in mid-incubation (nests 2, 4, 6, and 8) are inconsistent with the expected sequence of development for new nests. Piping Plovers typically begin lining nest cups with pebbles before laying eggs and complete lining the nests soon after completing the clutch. Moreover, in one case (nest 4; Fig. 3) photographic evidence reveals a four-day sequence in which pebbles are present in either the previous or the new nest cup, but not both.

Our observations are consistent with movement of eggs by adult Piping Plovers at four nests (nests 1–4), but for nests 5–8 our evidence is circumstantial. In two cases apparently initiated by the plovers (nests 2 and 3), the eggs were moved prior to inundation of the original nest site. Because nest 1 was located on a sandbar of a flowing river, the current associated with flooding suggests the eggs were moved prior to inundation of the original nest site. Also, because of the pyriform shape of Piping Plover eggs and physical features of the nest sites (e.g., conical cup, flat terrain, pebble lining, and ridges at the edge of nest cup), it is unlikely that Piping Plover eggs accidentally rolled out of these nests or nest 4. Because we observed erosion and wrack in the area, however, we can not rule out the possibility that nests 6–8 were inundated and the eggs were displaced then the adults subsequently gathered them in a new location. Our observation of eggs washed up on the shoreline suggests this scenario for nest 5. The rate of water-level increase coinciding with the observations between 10 and 15 June 2008 was the greatest of any time during the two years of our study (U.S. Army Corps of Engineers 2008). Therefore, we were less likely to directly observe evidence relative to the motivation of nest moves in 2008.

In these areas human activity other than research is rare; it is unlikely that the public moved nests or that disturbance by

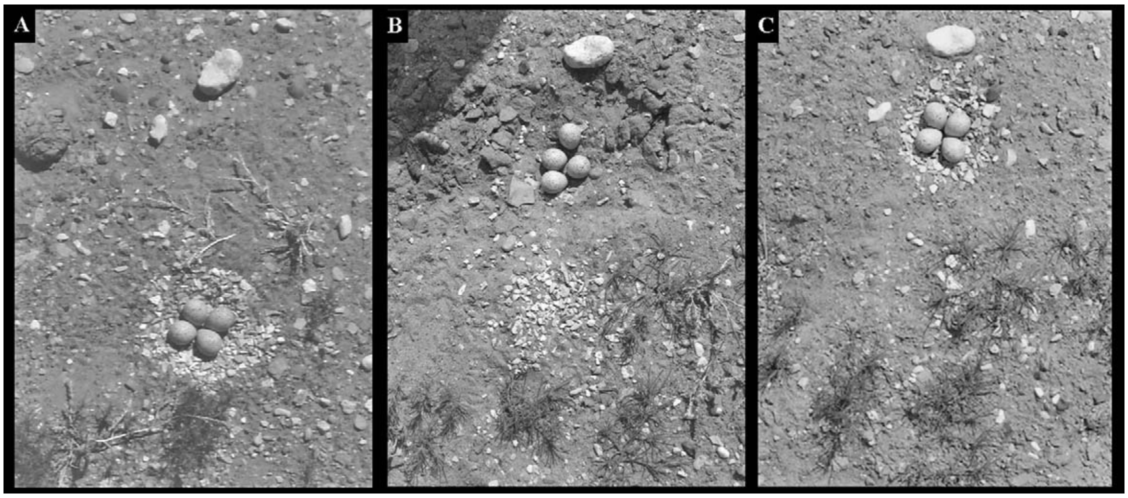

FIGURE 3. Chronological series of photographs documenting the movement of a Piping Plover nest after disturbance of a cattle hoofprint at Lake Sakakawea: (A) 20 June 2007, prior to the disturbance; (B) 2 July 2007, after the eggs were moved but prior to reconstruction of nest cup; (C) 4 July 2007, after the nest cup was reconstructed with pebbles in the new site.

researchers or the public motivated the observed movements. We intensively monitored 411 nests in 2007 and 2008 and observed movement of eggs only in cases where changes in habitat conditions were also evident. As part of the COE's management of the Piping Plover in this region, biologists sometimes move nests they perceive to be at risk of flooding short distances to less vulnerable locations (Prellwitz et al. 1995, Gordon and Kruse 1999). However, after speaking with COE staff and reviewing their field notes, we determined that their intervention was responsible only for the move of nest 3 from the second to the third nest site (Fig. 2; G. A. Pavelka, U.S. Army Corps of Engineers, pers. comm.). Additionally, the unaccounted distance (>2 m) between the 19 June location and the COE's relocation of nest 3 on 21 June suggests a potential second nest move by the adult Piping Plovers, prior to the COE's moving the nest.

Kenyon (1949) reported that an inundated American Oystercatcher (*Haematopus palliatus*) nest was moved twice over three days to avoid encroaching high tides; an adult oystercatcher was observed rolling eggs a short distance by using the tip of its bill. Waterfowl have also moved nests as a result of changing water conditions in the nest area (Avitabile 1969, Fleskes 1991) and as a result of being trapped on nests by researchers (Oring 1964, Johnson and Kirsch 1977, Blohm 1981, Hill 1985). Additionally, movement of eggs between clutches has been documented in waterfowl (Prevett and Prevett 1973, Duebbert et al. 1983, Duncan 1984, Lank et al. 1991). Calder (1926) reported the movement of a Killdeer (*Charadrius vociferus*) nest after he moved it atop an earthen mound (~0.3 m in height) to prevent inundation; the adult apparently made a new nest at the base of the mound and moved the eggs. White et al. (2009) reported observing an adult Piping Plover return an accidentally displaced egg back to the nest.

Our results provide the first documented evidence of nest movement, independent of direct anthropogenic manipulation, in a small-bodied (<500 g) precocial species and are notable for several reasons. First, complete clutches were moved in six of eight cases, and evidence also suggested that in at least one case (nest 4) nest lining was moved from one nest cup to another. Second, distances over which some adults moved their eggs (4.0 and 4.7 m for nests 1 and 3, respectively) were substantial and probably represented a physical challenge because of the pyriform shape of Piping Plover eggs, the size and shape of the Piping Plover's bill, and the uneven terrain. Third, of the four nests whose movements were apparently initiated by the adult plovers, two (nests 1 and 4) were successful and the other two were incubated by adults at their new upslope location until they failed because of rising water levels.

Rising water levels during the nesting season can increase the likelihood of nest inundation, requiring incubating adults to evaluate their reproductive options within that breeding season, including (1) initiating a new nest after inundation, (2) preparing for migration instead of renesting; or (3) moving a nest, prior to inundation, to a less threatened location. Multiple components of reproductive investment likely influence this choice, including the timing of the disturbance within the breeding season, the incubation stage, and the availability of suitable habitat for a replacement nest or a relocated nest. Piping Plovers commonly renest after nest failure early in the breeding season (Elliott-Smith and Haig 2004), but if a late nest is threatened there may not be time to renest, which could prompt more proactive measures to protect the existing nest, as seen in some nesting waterfowl (Avitabile 1969, Fleskes 1991). Each of our nests was >10 days into incubation when it was moved, suggesting a threshold beyond which parental investment makes protection or recovery of the nest a priority higher than renesting (Montgomerie and Weatherhead 1988).

We conclude that adult Piping Plovers are capable of moving eggs and recreating nests in new sites during incubation. Our results suggest Piping Plovers have the ability to perceive imminent threats to nests and evaluate their current reproductive investment in relation to alternative actions (e.g., renesting); these behaviors are consistent with prospective action (cf. Raby et al. 2007) to maximize reproductive fitness. For nests 5–8, however, we cannot rule out the possibility that eggs were gathered after being displaced by rising water, which would be more consistent with a reactive behavior. Regardless of the catalyst for egg displacement, at all eight nests the adults exhibited resilience by continuing incubation and recreating a nest cup lined with pebbles after the relocation.

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