ABSTRACT. In addition to feeding on fish at the water surface, the Brown Pelican (Pelecanus occidentalis) exhibits a range of diving attacks that include a unique form of high plunge diving. The high plunge dive begins with normal, upright flight and with prey detection the Brown Pelican will shift into a dive and often complete an aerial 180 degree counterclockwise rotation of the body prior to water entry. After inverted water entry, the bird follows a simple but shallow 180 degree half-loop underwater and returns to the surface upright near where it entered, but in a direction opposite that of the original flight path. This curious plunge diving behavior has hitherto remained inexplicable but has similarities to the Split-S air combat maneuver in human aviation. The Split-S also begins with normal, upright flight that enters a 180 degree inverted dive and ends with a 180 degree half-loop. When used offensively in air combat the Split-S is a hunting tactic wherein a pilot identifies a target directly below and rolls 180 degrees to an inverted attitude. Inverted diving is one of the quickest ways to stop forward air speed and convert it to a downward direction. It also allows visual contact with a moving target throughout the dive. A 180 degree half-loop at the end naturally restores the 180 degree inversion to an upright attitude, albeit opposite to the original flight path.

RESUMEN. Adicionalmente a alimentarse de peces en la superficie del agua, Pelecanus occidentalis, muestra una variedad de ataques, entre los cuales incluye una forma única de zambullirse desde la altura. La zambullida se inicia con un vuelo vertical normal y con la detección de la presa el pelicano se mueve hacia la posición de ataque y con frecuencia completa una rotación aérea del cuerpo de 180 grados en contra de las manecillas del reloj antes de entrar al agua. Luego de entrar al agua en posición invertida, el ave realiza media vuelta sumergida simple pero superficial de 180 grados y retorna a la superficie en posición vertical cerca del sitio de entrada, pero en dirección opuesta a la ruta de vuelo original. Este curioso comportamiento de la zambullida ha sido hasta el momento inexplicable pero tiene similitudes con la maniobra de combate de S dividida en aviación humana. La maniobra de la S dividida también comienza con el vuelo en posición vertical y entra en una zambullida en posición invertida de 180 grados que termina con media vuelta de 180 grados. Cuando es usada ofensivamente, la maniobra de combate de S dividida, es una táctica de cacería donde el piloto identifica el blanco directamente debajo y rueda 180 grados hacia una posición invertida. La zambullida invertida es una de las formas más rápidas de parar la velocidad del viento hacia adelante para convertirla en la dirección hacia abajo. También permite contacto visual con un blanco en movimiento a lo largo de la zambullida. La media vuelta de 180 grados al final, naturalmente recupera la inversión de 180 grados hacia una posición vertical pero en la dirección opuesta a la trayectoria de vuelo original.

Key Words: Brown Pelican; Pelecanus occidentalis; plunge diving; Split-S

INTRODUCTION

There are eight species of pelican worldwide. All are primarily piscivorous, but their prey capture reveals two different tactics. Whereas all eight pelican species can feed from the water surface by capturing fish in a gular pouch, only the Brown Pelican (Pelecanus occidentalis) and Peruvian Pelican (P. thagus) also include aerial plunge diving (Nichols 1918, Jaramillo 2009). The Brown Pelican, for example, is not only known for plunge diving, but doing so while inverted (Nichols 1918, Schreiber et al. 1975). Plunge diving is not unique to pelicans, but entering the water inverted is an inexplicable behavior not reported for any other bird species. Interestingly, based on genetic analysis, the Brown and Peruvian Pelicans are actually sister species in a clade not shared by the other six species (Kennedy et al. 2013). Thus, if feeding tactics were superimposed on that genetic analysis, the ancestral feeding state in the Pelecanidae is most likely surface feeding, and plunge diving is likely a shared derived trait that has evolved only once within that group. Whether the Peruvian Pelican also inverts while plunge diving is unknown.

The feeding plunge of the Brown Pelican is a common sight on the Gulf, Atlantic, and Pacific Coasts of North America. The plunge is rapid, reaching 18 m per second (Johnsgard 1993), and may take less than a second. During the aerial part of a high dive there is a rotation of the body, often to a 180 degree inverted aspect, just prior to water entry that occurs so rapidly it is difficult to observe with the unaided eye. Thus, the Brown Pelican starts its high dive upright with its feet down, but ends the plunge into water inverted and its feet up. To our knowledge, Nichols (1918) was the first to report this aerobatic inversion and that it precedes an even less frequently recognized 180 degree reversal that occurs just under the water surface. Following the underwater reversal, the bird often surfaces in a direction opposite to its original flight path.

There are myriad groups of phylogenetically diverse birds that swim underwater after prey and are called pursuit divers. The pursuit divers can be grouped into those that start the underwater dive while at the water surface such as anhingas, grebes, penguins, and puffins, and those such as boobies, gannets, kingfishers, pelicans, terns, and tropicbirds that are plunge divers, i.e., they begin the dive headfirst from the air before water entry. Among the plunge divers, all but the Brown Pelican enter the water upright, i.e., the dorsum is up and the venter is down, and we can
find no report that describes a body rotation leading to an inverted entry (Machovksy-Capuskas et al. 2012, Chang et al. 2016, Holbech et al. 2018, Crandell et al. 2019, Eliason et al. 2020). Upon water entry, these plunge divers that enter the water upright actively swim after their prey and where they surface will depend solely on prey pursuit and has little correlation to where or how they entered the water. Conversely, the Brown Pelican has been reported to rotate its body to inversion, i.e., the dorsum is down and the venter is up, during the plunge dive prior to water entry as a natural part of its behavior (Nichols 1918, Schreiber et al. 1975). Moreover, its water penetration is shallow and the bird undergoes a quick reversal and surfaces virtually at the site of entrance, but in the opposite direction of the original flight path (Nichols 1918).

Nichols (1918) and Schreiber et al. (1975:651) both noted that the Brown Pelican rotates its body during the aerial portion of the plunge dive and enters the water inverted, but the only comment from the former for the curious behavior was that it is an effect of the wind and for the latter that it rotates to “correct to right or left in a fast dive.” Nichols (1918:21) also noted the underwater reversal and the explanation given was that pelicans fly with the wind and the reversal prepares the surface bird for “instant” takeoff against the wind. However, following a dive, surfacing Brown Pelicans can have 5–8 kg of water and fish in their pouch, two or three times the weight of the bird itself, which require up to a minute to process (Schreiber et al. 1975). This time to process the catch would seem to obviate any reasonable opportunity for a rapid takeoff in many instances. Further, there is no explanation by Nichols (1918) or Schreiber et al. (1975) as to why either of these unique behaviors of inversion and reversal is important for a feeding Brown Pelican but unavailable to the same bird that simply lands on the water surface. So, it begs the question what is there about a diving Brown Pelican that warrants an inversion and reversal that could not otherwise be achieved at the surface with a deft kick of either webbed foot.

METHODS

We observed the diving behavior of Brown Pelicans in Belize and in the coastal states of Louisiana, Mississippi, and Florida within the United States. Much of the plunge dive was so rapid that it confused the unaided eye, thus we used high speed photography to examine the position of the bird in different aspects of the aerial dive with concentration on the high plunge dive. Because much of the underwater aspect of the Brown Pelican dive occurred just at the surface, sometimes with the bird only partially submerged and at much lower speeds, those observations were made with the unaided eye.

Photography for interpretation of the aerial dive was done either with Canon 7d mk2 with Tamron 100-400 mm lens generally at 400 mm or Nikon D-500 with Nikkor 600 mm prime lens. Exposure speeds necessary to capture the Brown Pelican plunge dives without blur were generally 1/3200 to 1/6400 of a second or greater.

While photographing the Brown Pelican in high plunge dives we had the occasion to make other observations on the feeding tactics of this bird and we categorized them into four groups. Category 1 represented birds feeding opportunistically at the water surface while floating. Category 2 were Brown Pelicans diving from low altitudes of less than 4 m above the water surface that did not include body rotation and ended as awkward splashes on the surface with head and neck penetration only. Category 3 were dives from low altitudes of less than 4 m above the water surface that included body rotation approaching 120 degrees, partial body submergence and partial reversal of direction upon surfacing. Category 4 represented Brown Pelicans plunge diving at heights greater than 4 m, almost always near 180 degrees of inverted rotation at water entrance, full body submergence and completing a simple, half-loop reversal underwater.

Determining age group of birds was done with a modified method of Carl (1987) in which birds with white bellies were considered juvenile and those with black bellies were considered adult. Dive height estimation was also done by the method of Carl (1987), which used wing span to estimate dive height from the beginning of the dive when wings were set to the water surface. That study used 2 m as a standard wing span for the Brown Pelican and we followed that method.

RESULTS

General observations

Our first observations on the rotation and inversion of the Brown Pelican were serendipitous and occurred in water approximately 30 km off the coast of Placencia, Belize near Ranguana Caye at noon on a sunny, still day in April. Our observations were made from kayaks. As many as 30–40 birds at any given time were floating and occasionally making stabs at fish from the water surface (Category 1). Some of these birds in Category 1 would take off and join the aerial attacks and be replaced by those from aerial attacks that remained on the surface following a dive. Approximately 60 juvenile and adult Brown Pelicans (ratio estimated at 1:2) were plunge diving at any given time within 20–30 m of us for over an hour. Although difficult to interpret with the unaided eye because of the speed of the dives, it was clear that the birds were undergoing a body rotation prior to water entry. It was also clear that all of the body rotations were being done in a counterclockwise direction. Eighty-five dives were counted to determine approximate height and frequency of the rotation. Among these dives only three (4%) could be classified in Category 2, nine (11%) were observed in Category 3, and 73 (86%) were in Category 4. Thus, irrespective of age class, 97% of the dives involved a counterclockwise rotation of the body, and 86% were approximating a 180 degree inverted entry. We had no way to identify individual birds and almost certainly observed some individual birds more than once.

The Belizean observations in Category 3 were typically of birds patrolling at low altitude that made dives at more acute angles than those in Category 4. The partial reversal in Brown Pelicans in Category 3 appeared because the head and neck impacted water first in a counterclockwise bank, while the body of the bird, still at high speed, pivoted about the head following the natural arc of the bank until it too struck and was slowed by the water. Brown Pelicans in Category 4 made their dives from greater height and at greater angles that sometimes approached vertical. The wings of birds in these Category 4 higher dives would initially fix perpendicular to the body but as the dive approached water would often transition rearward and trail behind the bird’s body as it struck the water. Even when the body completely submerged, the wing tips were frequently seen still above the water surface illustrating how shallow the dive was. Following successful dives,
Fig. 1. Composite photograph of a juvenile Brown Pelican (*Pelecanus occidentalis*) during a plunge dive showing the aerial counterclockwise rotation to 180 degree inversion at water entry. The second image illustrates the head still in an upright position despite the body in a 90 degree rotation. The last two images show how close to the water the final 90 degree to 180 degree rotation occurs. Photo by Eric Tilson, Boca Grande, Florida.

the Brown Pelicans were commonly observed to take up to a minute to process the water and fish.

In addition to general observations and photography done in Ocean Springs, Mississippi and Boca Grande, Florida, we also made a formal count of Brown Pelicans diving in a shallow lagoon in Grand Isle, Louisiana on an overcast, windy day in April. Those observations were made from land and the birds were at a distance of approximately 50 m. Fewer than five birds were floating on the surface stabbing at fish at any given time and they would occasionally take off and join the aerial hunt, and birds that had splashed down often took their place at the surface (Category 1). Approximately, 25 juvenile and adult birds (ratio estimated at 2:1) were plunge diving. Of 60 aerial dives counted, none occurred in Category 2, 54 (90%) occurred in Category 3, and six (10%) occurred in Category 4. Thus, although the majority of these dives occurred at a lower altitude than those observed in Belize, all of the dives included aerial rotation irrespective of age class and all were done in the counterclockwise direction. As noted with the Belizean observations, we had no way to identify individual birds and most certainly recorded some birds on more than one dive.

High speed photography and observations of Brown Pelicans in Category 4

High speed photographs of the plunge dive of a juvenile and adult Brown Pelican are shown in Figures 1 and 2, respectively, and a line-drawing of the essential elements is shown in Figure 3. Following detection of prey from altitudes of 4–19 m, the acute aerial aspect of the plunge dive began when the wings were set and no longer propulsive. When the wings were set, a counterclockwise body rotation began and not only did the pelican lose forward propulsion, but it also lost any natural lift the wings provided in horizontal flight. These two events caused the Brown Pelican to rapidly lose altitude and enter a dive. At that point, the speed and proximity to the water was such that the dive was rarely if ever aborted. As the bird accelerated the counterclockwise body rotation began and not only did the pelican lose forward propulsion, but it also lost any natural lift the wings provided in horizontal flight. These two events caused the Brown Pelican to rapidly lose altitude and enter a dive. At that point, the speed and proximity to the water was such that the dive was rarely if ever aborted. As the bird accelerated the counterclockwise rotation of the body approximated a 180 degree inversion as it entered the water. Never have we observed rotation beyond 180 degrees and never have we observed rotation in any but the counterclockwise direction.

Wind did not appear to have an impact on the behavior as the counterclockwise rotation and inversion occurred even when
there was no detectable wind and when there was wind, the rotation remained counterclockwise irrespective of the wind’s direction. Although the body only rotated counterclockwise during the dives, the head did not always follow until close to water entry. Thus, the bird prior to water entry from a high plunge dive can often be seen in photographs in a contorted position with a rotated body but upright head (as shown in Fig. 1 second image next to the top, and Fig. 2, next to last image). However, just before impact the neck was straightened and brought in line with the rotated body (as shown in Fig. 1, next to last image). The frequency of these events was not possible to count because they happened so quickly that we were never able to see them with the unaided eye. Even with our photographic methods, enough sequential images could not be taken to guarantee we did not miss such an event.

Whereas counterclockwise rotation of the longitudinal axis of the body was relatively fixed in the Brown Pelican high plunge diving behavior, the underwater half-loop was more variable and a complete reversal appeared to depend mainly on the degree of inversion upon entering the water. However, we also observed other factors that may have affected it that included different pitches of a moving water surface, the bird taking an out-of-plane stab at a fish, or the bird adjusting stress on the pouch because of different entry speeds. Otherwise, the simple half-loop appeared to be a natural consequence started in the air by the body rotation and the Brown Pelican continued a shallow arc till buoyancy returned them to the surface upright. The simple half-loop commonly occurred just under the water surface and the bird looked to rotate about the transverse axis of its body, i.e., along the wing to wing axis, before surfacing.

**DISCUSSION**

In our observations, Brown Pelicans fed at the water surface in similar fashion to all other pelican species and they also exhibited a range of aerial diving attacks that included a unique and curious form of plunge diving. The aerial attacks varied from heights just above water surface as they skimmed the waves or plunged from heights as high as 19 m. The attacks at altitudes of less than 4 m above water surface may or may not have included a rotation of the body prior to water impact. In those low altitude attacks that did not include rotation there was often an awkward splash at water surface with only the head and neck penetrating the water.
Fig. 3. The Brown Pelican (*Pelecanus occidentalis*) plunge dive. (1) Normal flight. (2) Beginning a counterclockwise 180 degree roll. This is the only direction this species will turn. (3) The roll is completed and the Brown Pelican is inverted prior to water entry. (4) The bird completes a simple, 180 degree half-loop underwater. (5) Normal upright attitude is re-established, but in a different direction and at a lower altitude than the originating flight.

Those low altitude attacks that did include some body rotation rarely showed full water penetration but often included some degree of reversal of direction following contact with water. Because the head and neck impacted the water first and slowed dramatically while in an incomplete inversion, it appeared that the body of the bird, while momentarily still at high speed, pivoted about the head following the natural arc of the incomplete twist until it too struck and was slowed by the water.

Only in dives of 4 m or higher did we observe body rotation reach full inversion and did a complete simple half-loop underwater reversal occur. When body rotation occurred it always was counterclockwise irrespective of height. Why the Brown Pelican only rotated in that singular direction is unknown. McSweeney and Stoskopf (1988) examined 14 Brown Pelicans at autopsy and found them to have lateral displacement of the trachea and esophagus to the right side of the neck. Thus, it could be conjectured that a counterclockwise rotation on water entry is a tactic that might protect structures on the right side of the bird.

Lateral displacement of both trachea and esophagus to the right-hand side of the neck is, however, not unique to the Brown Pelican. Klingler (2016) examined 42 phylogenetically diverse bird species and found that right-sided lateral displacement of both structures was the most common pattern in birds in his study, i.e., 38 of the 42 (90%) species showed that specific pattern. Klingler (2016) also showed a phylogenetic tree illustrating that right-sided lateral displacement of the trachea and esophagus was a basal trait in all birds, including the Pelecaniformes and all other groups where plunge-divers are found. Thus, if the counterclockwise rotation in the Brown Pelican is done to protect its right-sided trachea and esophagus during a plunge dive, it would be the only species among the plunge divers to do so even though those groups according to Klingler’s (2016) phylogenetic analysis are likely to have the right-sided condition, too. Most importantly, if protection of the trachea and esophagus is the purpose of the rotation, then that tactic should fail at a 180 degree rotation just as it would if the bird entered the water at 0 degree or no rotation.

Nichols (1918) noted the body rotation in Brown Pelicans and stated it was an effect of wind, but did not mention the direction of rotation. Schreiber et al. (1975) also noted body rotation and also did not mention its direction, however, the photographs of Brown Pelicans shown in his study were all diving in a counterclockwise rotation. Schreiber et al.’s (1975:651) interpretation was that rotation was for correction to the “right or left in a fast dive,” apparently not realizing that the Brown Pelican does not rotate clockwise in a dive and therefore cannot turn right. We have observed a full range of counterclockwise rotation from low altitude dives where the angle of water entry was acute and rotation may reach levels approximating 120 degrees to high plunges from 4–19 m and nearing verticality where rotation reached 180 degrees. We never observed a rotation beyond 180 degrees irrespective of height, which suggested to us that full inversion is the optimal attitude sought during a high plunge.

Following water impact, the degree of underwater reversal appeared to be largely determined by the degree of rotation entering the water. In water entries with body rotation reaching full inversion, the bird often completed a simple, 180 degree half-loop while the body of the bird was shallowly submerged and the tips of the wings could still be seen above water. We observed little underwater swimming following water entry. Given the bill shape and expansive gular pouch (Schreiber et al. 1975) and the extensive dermal pneumatic system (Richardson 1939) of the...
Brown Pelican it is understandable that it has limited underwater mobility and is one of the most restricted of the pursuit divers. Upon water entry, the bird slowed dramatically, but nonetheless continued the natural arc started by the inversion until buoyancy returned it to the water surface near where it entered, but in a direction opposite its original flight path.

Nichols (1918:21) reported that the Brown Pelican underwater reversal was a behavior that allowed the bird to fly with the wind and take off in an “instant” into the wind. Our observations were similar to his but do not support his conclusion. Many diving Brown Pelicans surfaced with a partial or full gular pouch and it was not unusual for a bird following such a dive to process the contents for up to a minute before flight as also previously reported by Schreiber et al. (1975). Thus it would seem unlikely that many pelicans have the ability or the need to immediately take off upon resurfacing. Perhaps most fatal to the wind explanation was that Brown Pelicans rotated to inversion and reversed when there was no discernible wind and when there was a wind they rotated counterclockwise no matter the wind’s direction.

Is there another way to understand the Brown Pelican diving behavior? There is an air combat maneuver in human aviation that also includes an inverted roll and dive, followed by a reversal of direction that is worthy of consideration (Shaw 1985). It is called a Split-S and a simplified version is shown in Figure 4. It begins with an idealized 180 degree roll of an aircraft, either clockwise or counterclockwise, to an inverted position. The 180 degree roll shown in the figure is not inviolate and may be modified to any degree to address the position of a given threat or target. While inverted and with the aid of gravity, the nose of the aircraft is pointed downward into a rapid dive and a 180 degree half-loop. Inverted diving is one of the most efficient tactics to reduce forward air speed and, with the aid of gravity, convert altitude into speed in a downward, vertical plane. The half-loop continues until a reversal is completed and level, upright flight in a direction opposite to the original is naturally re-acquired.

The Split-S can be used defensively to escape from a pursuer by diving and reversing to the opposite direction or, conversely, it can be used offensively when diving on a target that is observed at a lower altitude. That target can be contacted both in the vertical and horizontal aspects of the offensive maneuver. Because of the inversion, this tactic also has the advantage of allowing a pilot to visualize a moving target and make adjustments throughout the dive.

The plunge diving behavior of the Brown Pelican is clearly not defensive, but offensive as it is pursuing prey. When prey are identified below then a roll to an inverted dive would stop forward flight of a Brown Pelican rapidly as any lift provided by the wings would be lost and the potential energy of altitude would be converted into speed in a downward vertical plane. Time from the moment ephemeral prey at water surface are detected to contact just below the water surface is perhaps more critical to the Brown Pelican than any of the other plunge divers given its underwater pursuit limitations. In human aviation, the conversion of altitude into speed during such a dive can be so great that to protect the structural integrity of the aircraft or to prevent the loop from distending to the point of ground impact, pilots are taught to bring the throttle to neutral just prior to the dive and let gravity alone control acceleration. In a sense, the Brown Pelican does a similar thing by setting the wings at the beginning of the dive thereby stopping any propulsive motion of the bird itself and also letting gravity control the speed of the dive.

During the Split-S human maneuver, striking anything at the bottom of the dive, or anywhere else for that matter, would be catastrophic, but for the Brown Pelican striking the water is an essential part of its feeding strategy. No study has been done to assess how a Brown Pelican survives a 19 m plummet at 18 m per second but factors such as bill shape, long neck, and fusiform body likely reduce sudden injurious impact, and extensive dermal pneumatic air sacs likely cushion the blow to sensitive organs and structures (Richardson 1939). Richardson (1939:15) noted “The superficial air mattress of the [brown] pelican is strikingly developed on all of the bird’s ventral surface, including the neck and feathered parts of the head and extending out the wing even to the tip of the second digit.” Stresemann (1934) found that plunge divers such as pelicans, boobies, and tropicbirds have well developed dermal pneumatic air sacs and noted this is an adaptation to lessen impact with water, whereas that pnicacity is greatly reduced in non-plungers such as cormorants and anhingas that dive from the water surface. What other factors allow survival of the bird during a high plunge await elucidation.

At the end of an inverted dive, a man-made aircraft or pelican must at some point return to a normal, upright position. In dives of the aircraft and Brown Pelican, the 180 degree loop naturally and efficiently corrects the aerial 180 degree roll to inversion and returns both to an upright position.

When Figures 3 and 4 are compared, the Split-S maneuver in human aviation appears to have a symmetry that the Brown Pelican’s inverted maneuver does not. First, when the Brown Pelican fixes its wings and rotates it loses both forward propulsion and lift which cause it to descend immediately. A propeller or jet propelled aircraft can still have propulsive power while inverted and can even create lift if the wings are symmetrical and, therefore, may continue level, inverted flight briefly until throttle is reduced and the dive is started. Second, and most importantly, the human-directed Split-S is conducted throughout the inversion and half-loop in a single medium, air; whereas the Brown Pelican inversion begins in air, but the looped reversal is greatly condensed because of the bird striking and entering a much denser and viscous medium, water.

The Split-S air maneuver in human flight is well understood and has been used herein to offer some insight into aspects of the aerial inversion and underwater reversal observed in the Brown Pelican. First and foremost, when viewed from an offensive aspect, both are hunting techniques. Second, inverted diving is one of the quickest ways to stop forward motion and change to a downward direction following detection of ephemeral prey. Third, the inverted diving allows visualization of moving prey throughout the dive and to make continuous adjustments for contact. Fourth, the maneuver works with any target below the bird irrespective of the target’s heading. Fifth, the natural arc of a half-loop reversal would facilitate both the opening and filling of the pouch for prey capture. And sixth, completion of a 180 degree half-loop naturally corrects the aerial 180 degree inversion and restores both pilot and bird to an upright position, albeit in a different direction.
Lastly, convergent evolution is a phenomenon in which phylogenetically unrelated species have evolved similar adaptations, structural or behavioral, to similar ecological opportunities. From a behavioral standpoint, if you are a winged hunter and your prey is below and its position ephemeral, then a tactic like a Split-S makes sense for humans and perhaps even the Brown Pelican.

Responses to this article can be read online at: https://journal.afonet.org/issues/responses.php/64

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Data Availability:
We will make all relevant data, observations, and codes available.

LITERATURE CITED


