



Social learning in great white pelicans (*Pelecanus onocrotalus*): A preliminary study

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Abstract

Great white pelicans (*Pelecanus onocrotalus*) exhibit life-history parameters and ecological traits thought to be associated with social learning, and advanced cognitive processing more generally. In this study we investigated whether this species can acquire novel behavior socially in a foraging context. Birds from the test group watched a trained conspecific opening an opaque box containing a food reward by using its beak, whereas the control group had no demonstrator but saw the box for an equivalent time span. Individuals from both groups were subsequently allowed access to the box. Subjects of the test group performed significantly better than the control group. This is the first experimental evidence of social learning in a cooperatively hunting bird. Further studies are needed in order to shed light on the factors favoring the evolution of this capacity, by testing different pelican species that vary in their ecology.

Keywords Great white pelican · *Pelecanus onocrotalus* · Social enhancement · Social foraging · Social learning

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Introduction

Social learning, which involves observation of or interaction with others or their products, is crucial for numerous avian species and occurs in multiple different biological contexts (e.g., predator recognition, vocal learning, mate choice; for a brief review see Slagsvold & Wiebe, 2011). In what is probably the most extensively studied context, i.e. foraging (Griffin, 2004), we now know that many birds learn socially what, where, and when to forage (Lefebvre & Bouchard, 2003; see also Federspiel, Clayton, & Emery, 2009). Social learning also has a role in learning *how* to forage, such as tool use (e.g., Holzhaider, Hunt, & Gray, 2010), hunting skills (e.g., Kitowski, 2009), food-handling methods (e.g., Norton-Griffiths, 1967), or novel feeding techniques (e.g., Danel et al., 2018).

In addressing the latter aspect, a widely applied method involves comparing subjects that are allowed to observe an experienced demonstrator performing the behavior (e.g., opening a box with a hidden food reward) with other “naïve” individuals that do not receive a social demonstration (Hoppitt & Laland, 2008). This paradigm allows the testing of social influences on behavior and has been used in a range of different bird species, such as caracara chimangos, *Milvago chimango* (Biondi et al., 2010), pigeons, *Columba livia* (Bouchard, Goodyer, & Lefebvre, 2007), yellow-crowned bishops, *Euplectes afer afer* (Danel et al., 2018), greylag

geese, *Anser anser* (Fritz, Bisenberger, & Kotrschal, 2000), and keas, *Nestor notabilis* (Gajdon, Fijn, & Huber, 2004).

However, although social learning in the context of foraging has been described in numerous bird species, the possible drivers favoring its emergence and evolution are still unclear (Lefebvre, 1995; Lefebvre & Bouchard, 2003). For instance, long thought being an adaptation for group living (Klopfer, 1961), this capacity is also exhibited by less or non-social bird species (e.g., Western scrub jays *Aphelocoma californica*, Clayton Dally, & Emery, 2007; ravens *Corvus corax*, Fritz & Kotrschal, 1999; ruby-throated hummingbirds, *Archilochus colubris*, broad-tailed hummingbirds, *Selasphorus platycercus*, Altshuler & Nunn, 2001; white-eared hummingbirds, *Hylocharis leucotis*, Lara, González, & Hudson, 2009; see also e.g. Noble, Byrne, & Whiting, 2014, and Wilkinson et al., 2010, for experimental support in solitary non-avian species).

Another factor, i.e. diet, has also been suggested to affect social learning ability. The rationale is that generalist species may benefit more from gaining information about novel food types than specialists (e.g., Davis, 2008; Slagsvold & Wiebe, 2011). Similarly, opportunistic species should also exhibit better social learning capacities compared to conservative ones (Klopfer, 1961). However, both previous predictions have had counter-examples (Slagsvold & Wiebe, 2011).

Another possibility, i.e. territoriality, may prevent the emergence of social learning in birds (e.g., zenaida doves, *Zenaida aurita*, Dolman, Templeton, & Lefebvre, 1996; Lefebvre, Palameta, & Hatch, 1996; blue tits, *Cyanistes caeruleus*, Thompson, Ray, & Preston, 1996; bullfinches, *Fringillidae*, Reader, Hager, & Laland, 2011). Aggressive species are hypothesized to pay more attention to chasing intruders than to learning novel feeding behaviors from them, and opportunities to learn socially may be missing altogether if these species do not form social groups or pair-bonds (Lefebvre & Bouchard, 2003).

Therefore, the occurrence of social learning in birds may be facilitated if they exhibit social tolerance (Coussi-Korbel & Frigaszy, 1995) along with certain life-history parameters and ecological traits, such as longevity, prolonged parental care, or social foraging, that are thought to facilitate social learning in general (Gajdon, Fijn, & Huber, 2004; Gariépy et al., 2014; Ricklefs, 2004).

Great white pelicans provide an interesting biological model for investigating social learning in a foraging context. This largely unstudied species is endowed with features believed to favor social learning and advanced cognitive processing generally, i.e. a large relative brain size (the Lefebvre's "seventh group," Lefebvre et al., 1997; but see Logan et al., 2017), social foraging (Megaze & Bekele, 2013), and a slow life history including a long incubation period, longevity, and late sexual and physical maturity (Elliott, 1992; Hatzilacou, 1996).

Furthermore, in the wild, pelicans encounter many social learning opportunities. Outside the breeding season, they rest

in flocks during the day and gather in communal roosts at night (Elliott, 1992; Hatzilacou, 1996), which may serve as foraging information centers as proposed for other species (Ward & Zahavi, 1973). During the breeding season, they form large colonies (Guillet & Furness, 1985) and seem to copy one another by laying synchronously (Berry, Stark, & van Vuuren, 1973; Elliott, 1992; Megaze & Bekele, 2013). They also create protected crèches (10–100 individuals; Berry, Stark, & van Vuuren, 1973; Brown & Urban, 1969; Elliott, 1992; Evans, 1984) where juveniles stay in close proximity, which may influence the strong peer-attraction observed at maturity (Anderson, 1991; Clayton, Dally, & Emery, 2007). This may allow adults to engage in a rare behavior among birds: cooperative fishing (Anderson, 1991; Bowker & Downs, 2008; Din & Eltringham, 1974a; Din & Eltringham, 1974b; Elliott, 1992; Hatzilacou, 1996; Megaze & Bekele, 2013; Rand, 1954; Wirtz & Kacher, 1983; Wirtz, 1986). Importantly, pelicans have a prolonged immature period during which they continue to remain associated with their parents, who still feed them, potentially allowing the young to learn about this complex cooperative foraging skill socially (which requires a certain degree of experience; Burger, 1980), by closely observing skilled conspecifics. Social transmission of unusual and opportunistic feeding strategies (i.e., predation on seabird chicks) in the Western Cape has been suggested for great white pelicans (de Ponte Machado, 2007).

This study aims to expand the range of taxonomic groups studied with respect to social learning to a largely unstudied avian model, in order to further understand the possible drivers favoring the emergence and evolution of social learning in a broader comparative framework (Emery & Clayton, 2004). Indeed, adding to the comparative picture through the study of multiple species may allow identification of the potential life-history and ecological characteristics promoting this capacity.

To this end, we investigated whether the great white pelican was able to show social learning in the context of foraging. Five subjects had to learn a new foraging behavior by observing a conspecific retrieving a reward from a box (test group), while the other five individuals did not receive a social demonstration (control group). The apparatus used was conceptually similar to the one used by many previous studies exploring social learning in birds (e.g., Aplin, Sheldon, & Morand-Ferron, 2013; Biondi et al., 2010; Bouchard, Goodyer, & Lefebvre, 2007; Danel et al., 2018; Fritz, Bisenberger, & Kotrschal, 2000; Fritz & Kotrschal, 1999; Giraldeau & Lefebvre, 1987; Lefebvre, 1986). Although the social learning task reported here was not designed to distinguish among the different forms of social learning, the pelicans' life-history, behavior, and ecology led us to hypothesize that at least social facilitation (i.e., behavior resulting from the sheer presence of another animal or demonstrator; Zajonc, 1965) is operating in this species.

Methods

Subjects

Twelve adult pelicans were tested at a bird park in Villars-les-Dombes, France. Five were males (Cra, Cro, Hyd, Jac, and Jee), and seven were females (Asa, Bal, Coo, Her, Jan, Jani, and Jyw). All subjects belonged to the free-flight bird show and were brought down to 85–90% of their *ad libitum* weight during the high season of the zoo (from March to November), which was also the experimental period. All birds were maintained within an outdoor enclosure of two compartments (first compartment: $17.97 \times 5.88 \times 2.26$ m, including an indoor room: $2.34 \times 2.34 \times 2.26$ m; second compartment: $24.74 \times 17.91 \times 2.26$ m). Tests took place in the first compartment each morning from 8 a.m. to 1 p.m. maximum. Two birds were randomly chosen to be the demonstrators: “Jan” was the demonstrator for Jac and Coo, and “Jani” was the demonstrator for Asa, Jee, and Jyw. The tests began when these two birds could routinely solve the task in less than 25 s. The remaining ten subjects were assigned to two different groups: a control group (Bal, Cra, Cro, Her, and Hyd) and a test group (Asa, Coo, Jac, Jee, and Jyw). The social rank of each subject (dominant, subordinate, middle rank) was balanced between the two groups. The social rank of the demonstrators (Jan and Jani) was subordinate and dominant, respectively. The subjects had not been tested in any cognitive tasks previously.

Apparatus

The apparatus consisted of an opaque wooden box ($25 \times 25 \times 33$ cm) stabilized in the center of a platform ($54.3 \times 36 \times 1.1$ cm), and fixed with four wooden sticks ($25 \times 1.1 \times 2$ cm) (Fig. 1). The reward, a fresh common roach *Rutilus rutilus*, which was always placed in the middle of the box (12.5 cm from each side), could be obtained by sliding the lid either towards or away from the subject’s body.

Procedure

Test group Before each trial, the subject (observer) was transferred into a room with opaque walls, except for a removable grid wall in the front, from which it could witness the social demonstration. The apparatus was then presented to the demonstrator in front of the grid wall of the room, which rapidly pushed the lid and inserted its beak into the box. After the demonstrator had fed, the apparatus was placed in the center of the first compartment for a 15-min trial to test whether the isolated observer was able to reproduce the demonstrator’s behavior. Fifteen test trials were conducted for each individual in total (two trials per day). However, if a subject succeeded in opening the box, seven additional trials were administered after its first success to assess whether it continued to be

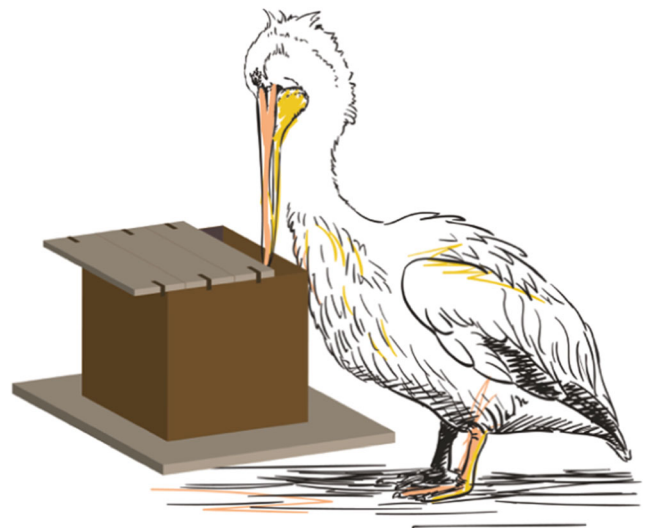


Fig. 1 Schematic representation of the apparatus used during the social learning task. The reward was located inside the opaque wooden box. In order to get the reward, subjects had to slide the top lid either towards or away from their own body. In the test group, the subjects (the observers) could see a demonstrator opening the box, whereas subjects in the control group could not see any demonstrator

successful in further trials (e.g., if a pelican opened the box in its second trial it was given seven other trials, i.e., nine trials in total).

Control group The same procedure as that of the test group was followed, i.e., the subjects were moved into the observation room for the same amount of time as those of the test group, so that the five subjects remained naïve (i.e., they had never seen the demonstrator opening the box before being tested).

Control procedure to measure individual neophobia We additionally implemented a neophobia test (Greenberg 1983) to control for the possibility that interindividual differences in interacting with the setup could not be explained by individual differences in neophobia. In this test, we randomly alternated the presentation of a novel object (test trial) and no object (control trial) next to a food container. We conducted these tests over five consecutive days (usually two trials per day, 2 h apart). Six trials were administered (each lasting 15 min maximum), three trials with a novel object and three trials with no object. The day before a trial, we randomly determined if the test trial or the control trial would be presented first. Before each test trial, the subject was isolated in a room, allowing the experimenter to place the novel object 12 cm away from a feeding dish located in the center of the aviary.

The novel objects consisted of three children’s toys: (1) a purple plastic hoop (80 cm in diameter), (2) a yellow duck figurine ($26 \times 25 \times 30$ cm), and (3) a black basketball (24 cm in diameter). These objects had never been presented to the pelicans before.

Data analysis

All tests were video recorded and continuous second-by-second coding of the videos was performed. Statistical analyses were performed using R version 3.2.3 (R Core Team 2015).

Social learning task In all videos we scored the trial number of each individual's first success, the latency to first success in seconds, and the number of successes that immediately followed on the first success.

Control procedure to measure individual neophobia The latency to feed in both control and test trials was recorded. The mean latency to take the food in test trials minus the mean latency to obtain the food in control trials served as the indicator reflecting the degree of neophobia. The mean values of this indicator were compared between all individuals and, separately, between test and control groups (Kruskal-Wallis tests).

Results

Social learning task

All subjects from the test group succeeded in opening the box, three of them at the first trial, and four subjects reproduced the behavior (at least five out of seven) during the seven subsequent trials (Asa, Coo, Jee, and Jyw; Table 1). In the control group, only one individual succeeded in opening the box during its last (i.e., 15th) trial (Bal), and this subject reproduced the behavior in three of the seven subsequent trials (Table 1). A significant difference was found between the performance

of the test group and the control group (Mann-Whitney U Test: $U=0$, $z=2.51$, $p=.008$). All successful subjects opened the box with the same technique as both demonstrators ("push"). In the control group, all subjects approached/touched the box, but they never tried to open it (except for Bal). Furthermore, the latency to approach and/or contact the box by these individuals did not correlate with individual neophobia (Spearman correlation test, $\rho=0.26$, $p=.65$). We also controlled for extra covariates, i.e. (1) time of day, (2) age, and (3) sex. (1) The repartition of tests according to time of day (i.e., early morning: 8–10 a.m., late morning: 10–12 p.m., early afternoon: 12–13 p.m.) showed no difference between individuals (chi-square test, $p=.99$) or between control and test groups (chi-square test, $p=.76$). (2) Mean age was 5.8 and 5.2 years for the test and control groups, respectively, with no significant difference (Wilcoxon test, $p=.27$). Individuals that opened the box ranged from 3 to 15 years old, and the tendency of younger individuals to solve the task in fewer trials was not significant (Spearman correlation test between age and number of trials before success on the six individuals, $\rho=0.57$, $p=.23$). (3) Sex had no impact on the success rate (Fisher exact test, $p=.63$) and there was no significant difference between the number of trials required to succeed between the sexes (Wilcoxon test, $p=1$).

Control procedure to measure individual neophobia

Most subjects irrespective of the group never approached the novel objects within the 15 min of the trial duration. The successful individuals from the test group did not seem the least neophobic; one subject from the test group (Jee) took the reward in the yellow duck figurine's condition, two subjects from the test group (Coo and Jee) and one subject from the control group (Hyd) took the reward in the purple plastic

Table 1 Individual performances of subjects from both the test and the control groups during the social learning task. The trial number of the first success, the latency to open the box during the first success, the opening

technique used both by demonstrators and successful observers, and the number of correct trials that followed the first success (replica) straight away are reported, respectively

Group		First success (trial)	Latency (s)	Replica ($n = 7$)	Technique	
Test	Dem.				Test	Dem.
Asa	Jani	3	00:34	5	push	push
Jac	Jan	8	00:54	3	push	push
Jee	Jani	1	00:25	7	push	push
Jyw	Jani	1	01:36	7	push	push
Coo	Jan	1	00:48	6	push	push
Control					Technique	
Bal		15	03:33	3	push	
Her		0	0	0	-	
Cra		0	0	0	-	
Cro		0	0	0	-	
Hyd		0	0	0	-	

hoop's condition, and one subject in each group (Jyw – test group; Cro – control group) took the reward in the black basketball's condition. By contrast, all subjects approached the food container in the control trials. Statistical analysis of the latency to approach the food container in controls versus tests revealed no differences between individuals and between control and test groups (Kruskal-Wallis test, $p > .05$ in both cases).

Discussion

Overall, our results showed that great white pelicans were capable of learning a new foraging behavior from their conspecifics, thus being able to exploit their environment by different means. Individual neophobia did not seem to affect the results since most subjects showed a neophobic response towards the novel objects regardless of their treatment group.

The social learning test reported here was a generic one that did not aim to distinguish between different learning mechanisms. However, some observations may suggest that social enhancement, the most frequent social learning mechanism observed during foraging in birds (Slagsvold & Wiebe, 2011), may be the plausible explanation. All birds from the test group approached and interacted with the foraging box while only one from the control group did so. We could then assume that the mere presence of the demonstrator elicited more interest towards the apparatus from the test group. These results are in line with findings on social learning in other avian species, where social enhancement has also been suspected to occur (e.g., yellow-crowned bishops, *Euplectes afer afer*, Danel et al., 2018; ravens, *Corvus corax*, Fritz & Kotrschal, 1999; white-throated magpie-jays, *Calocitta formosa*, Langen, 1996; Amazon parrots, *Amazona amazonica*, Picard et al., 2016).

Moreover, pelicans have many opportunities for this learning mechanism in the wild, which seems to appear mainly for feeding purposes (Burger, 1980). Tests with decoys, for instance, revealed that pelicans are strongly attracted by a foraging area because of the presence of solitary conspecifics or cooperative hunting groups (Anderson, 1991; see also de Ponte Machado, 2007; Hatzilacou, 1996; Wirtz, 1986). The increase in attraction to a specific location due to the presence of other conspecifics in this area is known as *local enhancement* (Thorpe, 1963, or if concerned with stimulus only, *stimulus enhancement*, Spence, 1937). In some species, these parsimonious, low-fidelity social learning mechanisms may be sufficient for cultural transmission over generations (e.g., Slagsvold & Wiebe, 2011).

High-fidelity social learning mechanisms (e.g., imitation learning), on the other hand, may depend on different factors, such as whether food is abundant in the environment, hard to access, hard to process, and also potentially on the

experimental design or procedure applied (e.g., simple vs. complex paradigms, dyadic or multiple two-action task settings; Picard et al., 2016).

Pelicans are largely piscivorous and possess one of the most highly specialized beaks among birds (Megaze & Bekele, 2013). Prey availability (i.e., local fish density) and access may depend on different external factors, such as overfishing in certain areas, feeding requirements of the chicks, fish spawning activity, fish movement on the water surface, or water area features (e.g., calm vs. turbid; Anderson, 1991; Hatzilacou, 1996). Where the fish are abundant, pelicans usually hunt on their own, while cooperative hunting is adapted to the more difficult problem of catching large fish in open water (Din & Eltringham, 1974a). In this context social learning may play a more significant role and the post-fledging crèche behavior (Anderson, 1991; Berry, Stark, & van Vuuren 1973; Brown & Urban, 1969; Evans, 1984; Elliott, 1992) might serve to exercise and develop cooperative fishing skills in juvenile pelicans through horizontal (via a non-parent model) and vertical (from parents to offspring) transmissions.

However, although this rare cooperative foraging technique (and sometimes innovative, see de Ponte Machado & Hofmeyr, 2004) is difficult to acquire (Burger, 1980), local enhancement coupled with social facilitation may be mainly required to perform this behavior successfully at maturity (Anderson, 1991). During cooperative hunting, young pelicans usually follow conspecifics, which are attracted by and land in the immediate vicinity of foraging groups of pelicans (local enhancement). Birds then form a circle, which they gradually reduce by beating their wings on the surface steadily to drive fish into the center of the formation. Once one bird begins to strike, the other flock members do likewise (social facilitation). When fish are sufficiently congregated, they finally strike the water with their beak *synchronously* in order to scoop the prey up (social facilitation, Anderson, 1991; Elliott, 1992; Wirtz, 1986).

Another argument for the involvement of such “low-level” social learning mechanisms in pelicans is that feeding in this species does not involve complex manipulation of prey per se. Similar to other non-extractive foragers whose diet does not include hard-to-process food, e.g., jackdaws (Federspiel et al., 2019), pelicans catch fish easily by simply dipping their bill into the water.

Therefore, although this study cannot rule out the possibility that emulation or imitation learning may be in play, social learning requiring social enhancement and social facilitation may be sufficient for pelicans to learn about novel foraging behaviors. Pelicans may need to use social information in order to locate *where* (e.g., Anderson, 1991) and *what* (e.g., de Ponte Machado & Hofmeyr, 2004) to eat, similar to other large-brained bird families tested, such as parrots and corvids (e.g., *Amazona amazonica*, Picard et al., 2016; *Corvus monedula*, Federspiel et al., 2019).

Taken together, our findings demonstrate that pelicans were readily able to modify their behavior in a foraging task based upon observation of an informed conspecific. We hope that this preliminary study encourages further investigations to ascertain the precise type of social learning mechanisms employed by this and other pelican species (Galef & Laland, 2005). More specifically, “higher-level” processes can only be entirely ruled out through the use of a two-action procedure (Zentall et al., 2004). The combination of group foraging, social tolerance and attraction, associated with specific life-history parameters (e.g., longevity, prolonged parental care), may favor the emergence of social learning in great white pelicans. In order to draw a proper conclusion, however, more comparative data are needed with closely related species that possess different ecological features. Future studies may also explore the importance of social learning in cooperative hunting animals by comparing great white pelicans and other cooperative hunters with closely related, but solitary fishing, pelican species (e.g., Dalmatian pelican *Pelecanus crispus*). It is our hope that the results presented here will encourage others to explore further social learning abilities in poorly studied avian species, in order to provide more comparative data.

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Open Practices Statements The data or materials for the experiments reported here are available from the corresponding author on reasonable request.

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