

Juvenile Galápagos Pelicans Increase Their Foraging Success by Copying Adult Behaviour

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Abstract

Social learning is the building block of culture and traditions in humans and nonhuman animals, and its study has a long history. Most investigations have addressed either the causation or the function of social learning. Though much is known about the underlying mechanisms of social learning, demonstrations of its adaptive value in a natural setting are lacking. Here we show that juvenile brown pelicans (*Pelecanus occidentalis*) can increase their foraging efficiency by copying adult diving behaviour, suggesting that social learning helps juveniles to find profitable food patches. Our findings demonstrate the potential fitness consequences of behavioural copying and thus highlight the possible adaptive importance of social learning.

Citation: Brumm H, Teschke I (2012) Juvenile Galápagos Pelicans Increase Their Foraging Success by Copying Adult Behaviour. PLoS ONE 7(12): e51881. doi:10.1371/journal.pone.0051881

Editor: Pier Francesco Ferrari, Università di Parma, Italy

Received: June 25, 2012; **Accepted:** November 12, 2012; **Published:** December 14, 2012

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Funding: Financial support was provided by the German Research Foundation (award Br2309/6-1), and the Association for the Study of Animal Behaviour (Christopher Barnard Award for Outstanding Contributions by a New Investigator to HB). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Social learning has fascinated sociologists, psychologists and biologists for a long time, and the last two decades have seen an explosion of both theoretical and empirical studies on social learning in animals [1,2,3,4]. In social learning, animals change their behaviour based upon information transferred from one individual to another. A prime example of social learning in animals is vocal learning [5] and vocal production learning in birds has been extensively studied [6,7,8]. Social transmission of behaviour can lead to copying [9], in which one animal matches the behaviour of another, thereby reproducing, for instance, patterns of movement or patch choices [10,11,12]. Behavioural copying is employed by many species to acquire foraging information [13,14,15,16]. Naïve fish, for instance, can learn the route to a food source by swimming with informed conspecifics, and in the process they copy the route from the other fish [17].

In the case of strongly heritable, species-typical foraging behaviour, vertical genetic transmission between generations takes place reliably and with high fidelity but on the other hand, such behaviour is also potentially less flexible in fluctuating environments. Various mathematical models have been developed to investigate the emergence of social learning in relation to non-social learning as well as the potential fitness consequences of social learning [18,19,20,21]. Another line of research attempts to link evidence for social learning with its value in the real world [reviewed in 13, 22, 23]. As far as foraging behaviour is concerned, such studies range from those which show the benefits of social learning in experimental situations in captivity that are designed to mimic real-world foraging problems, e.g. [24,25,26,27] to studies conducted in the wild with field experiments that have been seeded by an experimenter, e.g. [15,28,29,30,31]. However, only

few studies have demonstrated naturally occurring social learning in foraging animals in the wild. One notable exception is the work by Thornton & McAuliffe [32] who showed that adult meerkats provide pups with opportunities to practice skills of handling live prey, thus facilitating learning. In addition to the scarcity of field studies on naturally occurring social learning, previous research on foraging abilities has primarily looked at the acquisition of certain skills, such as solving a special task or handling a particular food item, e.g. [33,34,35]. However, to link social learning to survival and reproductive success, it is crucial to show that social learning improves vital foraging skills or foraging performance in general. Such a demonstration is imperative to a fuller understanding of the benefits of social learning in the wild, and, ultimately, may help elucidate the reasons that social learning has evolved in the first place.

Here we present observational data on the social effects on the general foraging efficiency in wild brown pelicans (*Pelecanus occidentalis*). In particular, we show the value of the presence of an experienced demonstrator for juveniles which must master the species-typical foraging technique known as plunge diving. In many animals, the juvenile phase is a critical period both in terms of survival and social learning [8,36,37,38]. Juvenile brown pelicans (Figure 1a) have a lower foraging efficiency than adults [39,40,41] and as a result many juveniles die of starvation [42]. Thus, the rapid acquisition of hunting skills in this species is a crucial process and its outcome has decisive fitness consequences.

The brown pelican is the only pelican species that dives for fish: foraging birds fly slowly at about 9 m above the water surface and upon sighting prey, suddenly check their flights and dive bill first into the water [43]. This so-called plunge diving (Figure 1b) is a challenging task because in addition to the evasive tactics of the

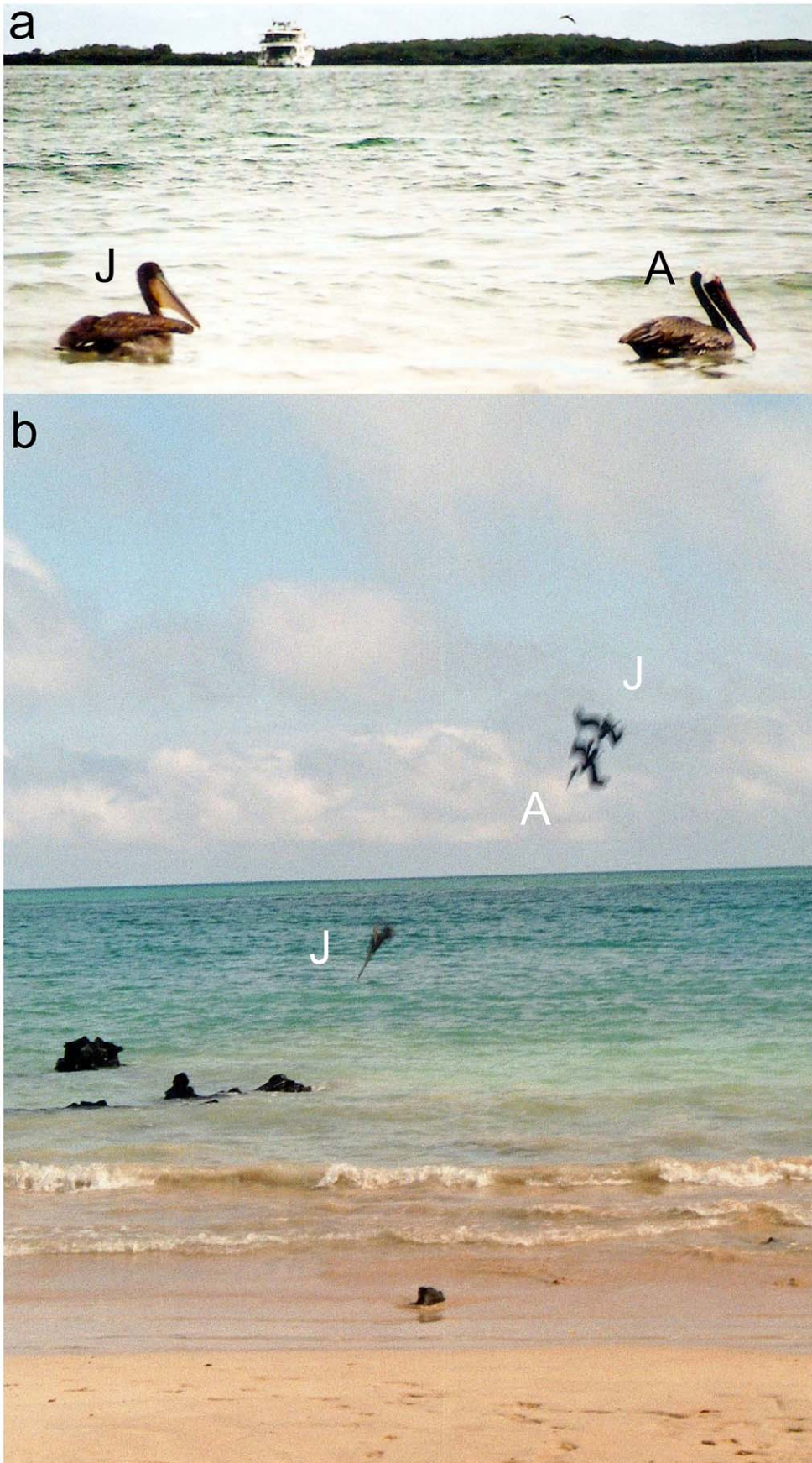


Figure 1. Brown pelicans (*Pelicanus occidentalis*) in the Galápagos Islands. a, age classes can easily be distinguished by their plumage: juveniles (J) have dark-brown heads and necks whereas adults (A) have white heads. **b**, plunge diving pelicans hunting for fish: a solo diving juvenile (centre) and a juvenile following an adult (right). doi:10.1371/journal.pone.0051881.g001

prey, diving pelicans must contend with other obstacles such as surface glare, refraction, and wind. The inferior foraging performance of juveniles hints at a deficit in the motor skills necessary for diving and catching fish or a lack of experience in selecting profitable food patches or both [44]. Since the juvenile period is a critical ontogenetic bottleneck because of the starvation risk [42] it is crucial for the survival of young pelicans to rapidly develop efficient hunting techniques in the transition to adulthood. Here we provide observational evidence suggesting that social learning may play a decisive role in the improvement of the general foraging efficiency of immature birds.

Methods

We studied the hunting behaviour of brown pelicans in the Galápagos Archipelago in January 2008 and February 2009. Mixed groups of adults and juveniles were observed at six different locations in the coastal waters of the islands of Santa Cruz, Baltra, and Isabella. The distances between the observing locations ranged between 20 and 96 km. Pelican group sizes varied between 3 and 17 birds with a mean number of 3.2 adults and 4.3 juveniles per group (ranges: 2–4 adults and 1–13 juveniles). Age classes were determined by plumage. Brown pelicans commonly acquire adult plumage around two years of age. Birds having dark-brown heads and necks were classified as juvenile, birds with white heads and necks were classed as adults [39,40]. The observed groups included all individuals that foraged within eyesight range at a given location. In all six cases, the groups remained constant during the entire observation period, i.e. no bird left the location and no new bird joined the group.

All foraging was confined to within 30 meters of the islands, and could be observed from shore without the aid of binoculars. The hunting behaviour of the pelicans at each location was continuously observed and all plunge dives and their outcome were recorded in a field notebook. At each location, all observations were made during one day and each location was only visited once. Three locations were visited in the morning between 0600 and 1100 hours and three sites in the afternoon between 1400 and 1700 hours. Average observation time was 86 minutes per location (range: 35–120 minutes). In total, 532 diving events were observed (151 dives by adults, 310 by juveniles, 71 by juveniles copying an adult).

The success of pelican plunge dives is easy to score because a toss of the head is indicative of swallowing [39,43]. If no catch is made, birds pull their heads out of the water with the bill open, allowing the water to drain out immediately, and the head and bill rapidly return to the normal position. Successful birds, on the other hand, drain the water from their bill slowly, and then swallow their prey by tossing the head backwards.

Before diving, foraging birds fly slowly above the water surface at a height of about 9 m, looking for prey [45]. Usually, the search flights of different birds do not seem to be spatially coordinated but sometimes a juvenile may closely follow a hunting adult (usually within a few meters). When the adult is diving, the following juvenile will dive immediately after it, so that its bill will enter the water surface within 1 or 2 meters from the preceding adult. Based on prior observations, we used an operational criterion of diving within 1 second after the adult. At five of the six study sites, only

four or fewer juveniles were observed and all of these dived on their own as well as with an adult.

We investigated differences in foraging success between adults, juveniles, and juveniles following adults with generalized linear mixed-effects models (GLMMs) calculated in R 2.10.1 (R Development Core Team 2009). As we could not distinguish individuals in all cases, we included site as a random effect rather than individual. Thus, the overall sample size was $N=6$ study sites. The GLMMs were fitted with a binomial error structure, using the function `lmer` (R package `lme4`). We used a model comparison approach (Wald χ^2 test) to assess whether omitting the factor “group” from the model caused a significant change of the model fit. As post hoc tests, we quantified the strength of evidence for differences between classes of pelicans with simultaneous tests for General Linear Hypotheses, using the `multcomp` package in R [46].

Ethical Statement

This field study consisted solely of observations from publicly accessible sites of the Galapagos National Park. Both researchers had permits to enter the national park. Animals were not manipulated or otherwise disturbed through these observations. Therefore, no special permit was required for this study.

Results

We found that the pelican classes (adults, juveniles, and juveniles following adults) differed markedly in their hunting efficiency (Wald test: $\chi^2=63.3$, $df=2$, $p<0.0001$, see Figure 2), with juveniles having a lower hunting efficiency than adults (estimate: -1.6930 , SE: 0.2261 , $z=-7.487$ $p<0.001$). However, we also discovered that juvenile birds sometimes copied adult fishing behaviour. In these instances, juveniles followed a hunting adult closely, immediately following adult dives and plunging into the water within 1 or 2 meters of the same spot (Figure 1b). Such behavioural matching was frequently observed, with juveniles following an adult in 23% of all their dives. However, we never observed that an adult bird copied the diving behaviour of another adult nor that a juvenile copied another juvenile.

There was strong evidence that copying adult behaviour increases the foraging success of the juvenile pelicans (estimate: -0.9765 , SE: 0.2792 , $z=-3.498$, $p=0.001$, see Figure 2): When diving on their own, juveniles caught fish on an average of 33% (95% CI = 0.22–0.46) of all hunting attempts (estimated average success rate as estimated from the model), but they raised their proportion of successful plunge dives to 57% (95% CI = 0.39–0.73) when reproducing the adult fishing behaviour. However, even the increased hunting success of socially foraging juveniles was below adult performance (estimate: -0.7165 , SE: 0.3018 , $z=-2.374$, $p=0.045$, see Figure 2). The foraging success of the adults was not affected by the presence of a juvenile (Wald test: $\chi^2=0.57$, $df=1$, $p=0.449$).

Discussion

We observed that juvenile brown pelicans substantially increased their hunting success when copying adult diving behaviour. This increase in juvenile foraging efficiency in the presence of an adult suggests that the poorer hunting success in juvenile birds

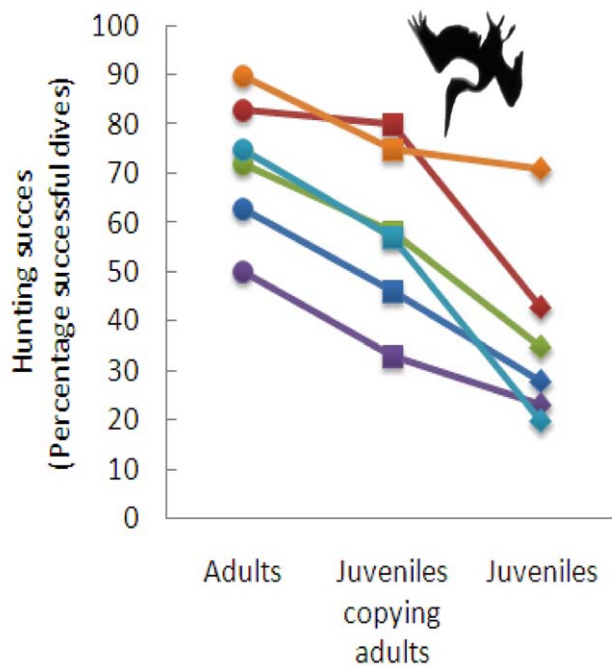


Figure 2. Foraging success of adult and juvenile brown pelicans. Data are shown for all six study sites. doi:10.1371/journal.pone.0051881.g002

is not entirely attributable to a lack of the motor skills necessary for capturing fish. Instead, immature pelicans may be less capable of correctly evaluating the profitability of foraging patches, e.g. by assessing prey density. By copying the patch choice of adults, juveniles benefit from the adults' knowledge to recognize profitable feeding opportunities. It is most likely that this gain arises through the behavioural synchrony which leads to diving in the same spot. Knowledge transfer probably occurs in a second step, when the matching of adult behaviour enables juvenile birds to eventually learn to distinguish profitable food patches from unprofitable ones on their own. Both steps together would result in learning that is functionally equivalent to contextual imitation, where an observer learns to use an existing action in a novel context [47]. However, our data also show that even the increased foraging success of copying juveniles was below adult performance, which may reflect an age-related difference in motor skills. Thus, immature pelicans may increase their hunting abilities in two independent ways: profitable patch choice may be enhanced by social learning, whereas individual learning may be needed to improve physical foraging skills.

Alternative interpretations of our observation that do not require social learning may involve the notion that the probability of following a diving adult could be affected by the hunting skills of juveniles. For example, older juvenile pelicans might be both more likely to follow adults and more likely to successfully capture fish than younger juvenile pelicans, or juvenile pelicans that are more adept at catching fish might be more likely to follow adults. However, we are confident that these alternative hypotheses cannot explain our findings. At five of our six study sites, only a small number of juveniles were present (4 or fewer), enabling individual identification throughout the observation period, and all of these dived on their own as well as with an adult. This means that the overall effect of increased hunting success of copying birds cannot be attributed to different individuals engaging in social and individual foraging.

Many animals travel to and feed in locations where they can see conspecifics feeding [13]. This is an example of one particular mechanism of social information acquisition known as 'local enhancement' [48]. This process is important in finding and learning about foraging sites in many taxa, including birds, fish, mammals, and insects [13,49]. Local enhancement may also account for the observation that juvenile marsh harriers (*Circus aeruginosus*) increased their foraging success when they hunted in the same area together with adult birds [50]. The young harriers caught more prey when foraging not further away than 50 meters from an adult but, unlike in our study, the juvenile birds did not match the movements of the adult birds. Thus, it seems that juvenile harriers may be attracted by local enhancement to food patches where adults hunt but then they forage independently once they arrive there. A similar process of local enhancement and subsequent independent foraging has also been suggested for feeding great tit (*Parus major*) flocks [51]. However, local enhancement cannot account for the phenomenon reported here, since we did not observe that juvenile pelicans gravitated towards the location where they observed foraging adults per se, rather they closely followed an adult during flight and meticulously matched its diving behaviour. In other words, the foraging patch choices of the juveniles could not have been the result of their increased attention to the location where an adult dived because of the very short time lag of less than a second between the patch choice of the adult and the matched choice of the juvenile. Figure 1b illustrates how closely the observer foraging matches those of the demonstrator, both in terms of timing and location.

Other cases of patch choice copying that show similar matching in time and space were reported in laboratory studies with foraging fishes [52]. In particular, fish have been shown to follow informed individuals to find food patches [17]. Complex underlying social learning mechanisms need not be invoked in order to explain such guided social learning. Patch copying in fish or patch choice copying in plunge diving pelicans could be explained given certain prerequisites like the motivation to shoal in the example of the fish or in the case of the pelicans, social tolerance between a demonstrator and observer, along with the motivation of observers to replicate specific demonstrator motor patterns (contagion) and the ultimate attainment of a food reward upon accurate copying of behaviour [53]. Further work would be needed to elucidate the exact mechanisms involved in the development of pelican plunge diving behaviour.

To support our interpretation of the data, a crucial next step would be to follow individual juvenile pelicans over time to see whether there is an improvement in solo diving skill that is related to the degree of their previous association with diving adults. Regarding the transfer of socially acquired information between individuals it would furthermore be interesting to know from whom juvenile pelicans copy. The cases in which we could distinguish individual birds suggested that each juvenile only followed one or two particular adult birds, raising the possibility that young birds may learn from their parents. However, it is rather unlikely that the reported social learning of hunting behaviour in immature pelicans involves teaching [54], for we did not observe any signs of active facilitation of learning by the demonstrating adults (e.g. by slowing down their flight to ensure that the juveniles could stay in close proximity). Also, the adults did not suffer a reduction in foraging success because of the juvenile's presence.

The increased foraging success of copying juveniles in comparison to non-copying birds clearly indicates the potential fitness consequences of social learning. Beyond that, our findings highlight the adaptive importance of copying others, since

behavioural matching considerably improved individual hunting success in brown pelicans, which, in turn, will increase the probabilities of survival and reproduction.

Acknowledgments

We thank Kevin Laland and Sabine Tebbich, as well as Pier Ferrari and two anonymous reviewers, for their comments on a previous draft of the

manuscript. Mathias Ritschard and Mihai Valcu helped with the data analysis.

Author Contributions

Conceived and designed the experiments: HB. Analyzed the data: HB IT. Wrote the paper: HB IT.

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