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Social Learning in the Caracara Chimango, *Milvago chimango* (Aves: Falconiformes): an Age Comparison

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Abstract

Milvago chimango is a gregarious raptor showing great ecological plasticity. Their ability to explore new resources has allowed them to survive in areas with increasing human modification. In this study, we evaluated the social learning ability in wild-caught individuals of *M. chimango*. In particular, we tested whether an 'observer' individual could improve the acquisition of a novel behaviour by watching a 'demonstrator,' and we examined the effects of age of both observers and demonstrators on social learning. We measured the ability of 18 observers to open an opaque Plexiglas box containing food, and we compared their performance to that of 10 control birds who did not watch a demonstrator solve the task. Prior to watching a demonstrator, only two of the observers and two of the control birds were able to open the box. After watching a demonstrator, 67% of observers were able to open the box, outperforming control birds in speed and success. Juvenile observers were more successful and faster than adults at contacting and opening the box. The age of the demonstrator did not influence the observers' likelihood of success. These results showed that *M. chimango* are able to learn a box-opening task with a hidden food reward by observing the behaviour of a conspecific and that this behaviour persisted over several days. Social learning ability in *M. chimango* might allow certain behavioural patterns, such as those related to novel resource acquisition in modified environments, to be socially transmitted among individuals in a population.

Introduction

Learning is defined as a change in an animal that is caused by a specific experience at a certain time, which is detectable later in the animal's behaviour (Rescorla 1988; Heyes 1994). Through the process of learning, animals can acquire, store and subsequently use information about their environment. This information complements genetic information, allowing animals to adjust their behaviour to the particular conditions of their local surroundings. Learning, therefore, allows a degree of behavioural fine-tuning that would not be possible solely based on genetically coded information (Galef & Laland 2005).

Direct interaction with the environment allows animals to gather accurate, up-to-date 'personal or private information', the sources of which often do not respond directly to the behaviour of the information gatherer (Dall et al. 2005). Nonetheless, the acquisition of personal information (i.e. by exploration and trial-and-error learning) can be costly both in terms of time and in terms of energy that must be invested and the increased likelihood of being

exposed to a variety of risks, like predation and poisoning (Boyd & Richerson 1985; Galef 1993; Laland 2004; Dall et al. 2005). Alternatively, 'social acquired information' (Danchin et al. 2004) can be obtained by observing the behaviour of other animals, which might respond actively to the behaviour of the receiver (Dall et al. 2005). Individuals are assumed to benefit by copying others because by doing so they take a shortcut to acquiring adaptive information, saving themselves the costs of asocial learning (Galef 1995; Giraldeau & Caraco 2000; Laland 2004; Webster & Laland 2008).

Many species have evolved the capacity to use 'public information or social cues' (Valone 1989; Danchin et al. 2004) to guide their learning about their immediate environment.

Social learning is defined as any modification of the behaviour that is acquired at least to some extent, by paying attention to the behaviour of another animal or its products (Box 1984; Heyes 1994; Hoppitt & Laland 2008). In this way, many biologically important decisions that an animal must make can be affected by observing the behaviour of others. By copying others, for example, naïve animals can learn about novel resources, the location of valuable food and water sources, how to identify and avoid predators, and how to move safely and efficiently around their environment (Laland 2004).

To attain a full comprehension of social learning in nature, the underlying psychological processes must be first well understood. Several mechanisms may be responsible for social learning (i.e. Hoppitt & Laland 2008). Social facilitation, for instance, occurs when the mere presence of another animal or demonstrator, changes an animal's motivation, which can result in a change of the subsequent behaviour of the observer individual (Zajonc 1965). Also, the observation of the behaviour of a demonstrator may result in an increase in the salience of a particular stimulus or location within the environment for the observer, and may consequently increase the observer's motivation to investigate such characteristics. This mechanism is known as stimulus enhancement (Spence 1937) or, if concerned with location only, local enhancement (Thorpe 1963). Observational conditioning is defined as a kind of classical conditioning (stimuli-stimuli learning), where the observer associates the location or object with the reward obtained by the demonstrator at t_1, and exposure to this relationship effects a change in the observer detected, in any behaviour, at t_2 (Heyes 1994). Moreover, by observing a demonstrator's action an observer may learn about the potential uses (affordances) of a stimulus, a phenomenon known as emulation or learning affordances (Zentall 2004). In this type of learning, an observer does not necessarily learn about the actions themselves, but only its consequences, using its own techniques to achieve the goal. Contrarily, imitation is the observers' ability to learn the patterns of behaviour by observing the form of the demonstrator's behaviour (Heyes 1994; Zentall 1996). All these social learning mechanisms are not mutually exclusive but may synergistically support actions of the observer (i.e. Huber et al. 2001).

The ability to gather information and learn from others has also important implications for the transmission of new behavioural patterns or innovations, within a population, regardless of the specific learning mechanism involved. In fact, social learning and innovation rate are thought to be correlated processes in birds and primates, along with neophobia and individual learning (e.g. Lefebvre & Bolhuis 2003; Reader 2003). Because behavioural innovations are assumed to have significant fitness implications for the invasion and creation of new niches, the transmission of new adaptive behaviours may have, in turn, important evolutionary consequences for the species (Nicolakakis et al. 2003; Reader & Laland 2003).

Theoretical models suggest that indiscriminate copying is not adaptive and will not increase the mean fitness of individuals in the population (Boyd & Richerson 1985; Giraldeau et al. 2002; Laland 2004). On the contrary, animals should be selective with respect to the circumstances under which they rely on social learning and the individuals from whom they learn. In a landmark work exploring the relation between social dynamics and social learning, Coussi-Korbel & Fragaszy (1995) suggested that the social rank, age, sex, patterns of association and other characteristics of both demonstrators and observers or inexperienced individuals frequently influence the likelihood of social learning. As a result, information may be transmitted through subsections of animal populations at different rates. For example, Pongrácz et al. (2008) found that the perceived dominance rank has a strong effect on social learning in individuals within a dog group. Reader & Laland (2000) also noted a striking sex difference in the diffusion of foraging innovations in guppies (*Poecilia reticulata*). Similarly, the influence of other birds on chickens' *(Gallus gallus)* ability to learn about food unpalatability declines with age, probably because individual learning experience becomes more important (Nicol 2004, 2006).

Birds of prey (Aves: Falconiformes) are considered to be highly opportunistic and innovative species, with proportionally large brains and a high rate of behavioural innovation (Lefebvre et al. 1997, 2001; Nicolakakis & Lefebvre 2000; Nicolakakis et al. 2003). Most raptors are gregarious to some degree, relying to varying extents on social information about feeding and habitat resources (Ellis et al. 1993). In spite of these characteristics, few attempts have been made to analyse the behavioural and ecological factors that promote social learning in these birds. In this work, we evaluated the social learning ability in wild-caught individuals of a Neotropical raptor, the Caracara Chimango, *Milvago chimango*. We tested whether problem-solving ability (the capacity to open an opaque Plexiglas box with a hidden food reward) was improved by observing the behaviour of a trained demonstrator. The age of both observers and demonstrators was included in the analysis to assess the effect of this factor on the probability of social learning. *Milvago chimango* is a highly adaptable and gregarious raptor; it is the most common bird of prey over most of its range and is one of the most common raptors worldwide (Fergusson-Lees & Christie 2001). Its extremely opportunistic feeding behaviour and generalist diet may have influenced its success over its wide geographical range. Its broad diet includes arthropods caught in flight and from the ground, small mammals, reptiles, amphibians, birds and even plant material (e.g. sunflower seeds) and carrion (Cabezas & Schlatter 1987; Biondi et al. 2005). In urbanized areas, it feeds on urban prey and human waste. In relation to this habit, the chimangos have learned to open bins and bags to feed from rubbish, a novel behaviour related to the occupation of urban areas (Kark et al. 2007; Biondi et al. 2008). The gregarious habits of this species include the formation of breeding colonies and communal roosts, as well as age-mixed foraging aggregations. These behaviours are most likely related to their ephemeral and/or clumped food resources (i.e. insects or carrion) (Fraga & Salvador 1986; Fergusson-Lees & Christie 2001; Biondi et al. 2005). Because the social dynamics of an animal population may influence the likelihood of social acquisition of information and novel behaviours (Coussi-Korbel & Fragaszy 1995), it would be expected that the gregarious habits showed by this species might facilitate social learning about adaptive information. Moreover, in generalist species such as *M. chimango*, whose diet includes a wide range of food types, social learning about novel foods or the location of new feeding patches is likely to be especially beneficial, particularly for juvenile individuals, for which most resources are unfamiliar or novel (Klopfer 1961; Galef 1993; Lefebvre 2000).

Methods

Subjects and Housing Conditions

Thirty-two chimangos were caught with baited walk-in traps (Bloom 1987) in a suburban area (Buenos Aires Province, Argentina) during two non-reproductive periods (March–August 2008 and 2009). At the end of the experiments, all the individuals were released at the capture sites. Housing and care conditions followed Bloom (1987) and Aprile & Bertonatti (1996). The birds included in this study were 16 adults (older than 2 yr) and 16 juveniles (lesser than 1 yr); body plumage colour (mainly rectrices), tarsus colour and moult stage were used to determine age (see White et al. 1994; Fergusson-Lees & Christie 2001). After being captured, birds were identified with leg bands and housed in individual cages ($1.5 \times 1.5 \times 1.3$ m^3) in outdoor aviaries. The cages were visually isolated from each other by a black synthetic fabric, except during the observation phase Individuals were not isolated acoustically; control and observer birds were housed in identical conditions. Individuals were given a period of habituation to captivity. During this period, the birds were able to drink water *ad libitum* from a receptacle attached to their perch, and once a day they were fed with beef and chicken meat (60 g) presented in a plastic dish (20 cm of diameter and 5 cm of depth). The habituation period lasted until the individuals were comfortable enough to eat the food shortly after its presentation, without signs of stress or tension (approximately 1 wk).

Experimental Procedure

The chimangos captured were allocated to three groups: (1) observer group, with 18 birds (nine adults and nine juveniles); (2) demonstrator group, with eight individuals (four adults and four juveniles) and (3) control group, with 10 individuals (four adults and six juveniles). On several occasions, the same demonstrator was used for more than one observer (Table 1). Only four of the birds in the demonstrator group were trained by the researcher to open de operant box and act as demonstrators ('human-trained' in Table 1); the remaining four birds were the observers that showed the best social learning performance during the previous test. These

Table 1: Relationship between observers and their demonstrators showing the identity of demonstrators (column 1, Demonstrator ID), whether they were captured and trained by the researcher (human) or resulted from previous social tests (OB_i) (column 2, Demonstrator source), and the identity of the observers for which they acted as demonstrators (column 3, Observer ID)

Demonstrator ID	Demonstrator source	Observer ID
DM1	Human	OB1, OB2
DM2	OB1	OB3, OB4, OB5
DM3	OB4	OB6, OB7
DM4	OB7	OB8, OB9, 0B10
DM5	Human	OB11, OB12
DM6	OB12	OB13,0B14
DM7	Human	OB15, OB16
DM8	Human	OB17, OB18

observers were used as demonstrators for the next group of observers analysed (Table 1). During all experimental sessions, the subjects (controls and observers) were video recorded for posterior behavioural variables analysis.

Demonstrator training

The demonstrators were trained to open an opaque Plexiglas box (Fig. 1) that had two sliding lids, containing hidden food (small bits of meat, 30 g in total). To train these individuals to perform their task, we used a method of successive approximations, with each step of the shaping procedure resembling more closely the target task (open the box and eat the food). The training began with the exposure of the birds to a lid-less box containing the food. In this way, the individuals could learn to associate the box with a food reward. Once the subjects were seen to have fed from the box immediately after its presentation, in the following session, the box was presented with its lid, leaving a broad opening through which they could feed. Over the subsequent training sessions, the opening was progressively closed, leaving only a small aperture through which the bird could put its bill inside or grasp the lid with its talons. The last training step involved the presentation of the opaque box with the lids completely closed. If a bird failed to open the box during the 30-min session, it was presented with the box with the lids slightly opened in a single additional session 1 h after the failed session. During the next day, this bird was tested again with the box closed, and given additional partially closed box sessions if the bird again did not succeed in opening the box. Once a bird successfully reached the food from the closed box, it was presented with the box completely closed for four more days to ensure that each demonstrator continued to succeed in the task.

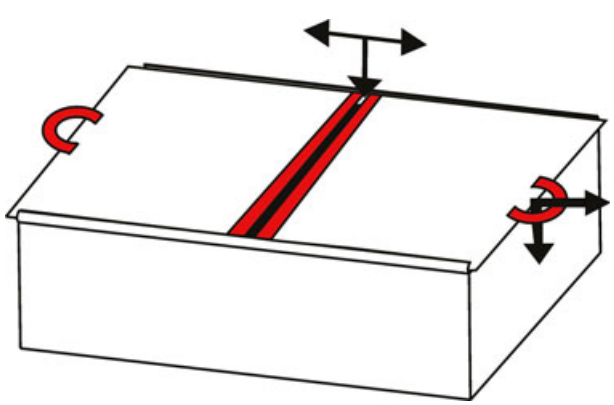

Fig. 1: Opaque Plexiglas box used in the social learning test. Arrows indicate the movement of the lids owing to the opening technique used by the birds.

First exposure to the operant box (D0)

After the habituation period ended, all observers were given a first 25-min session (D0), during which a closed Plexiglas opaque box containing food was presented to each individual. Because *M. chimango* has previously shown to be able to solve novel feeding tasks (Biondi et al. 2008, 2010), this session was included in the experimental design with the objective of checking for spontaneous openings. For each subject, the following variables were registered: *approach latency*, the time from first presentation of the box to initial approach (10 cm or less from the box); and *contact latency*, the time from the initial approach to first contact with the box (intentional contact). If the subject opened the test apparatus, two additional variables were recorded: *opening success*, the failure or success in opening the Plexiglas box and *opening latency*, the time from first contact with the box to successfully opening the box.

Observation phase

After D0, all birds experienced a break of 7 d during which they were not presented with any task. Following this period, the observers were confronted with a demonstrator for two 1500-s observation sessions per day (with an intersession interval of 60 min), for four consecutive days. During each observation session, the visual barrier (black synthetic fabric) between demonstrator and observer cages was removed, allowing the observers to see a demonstrator interacting with and opening the box to feed from the food inside it. All demonstrators

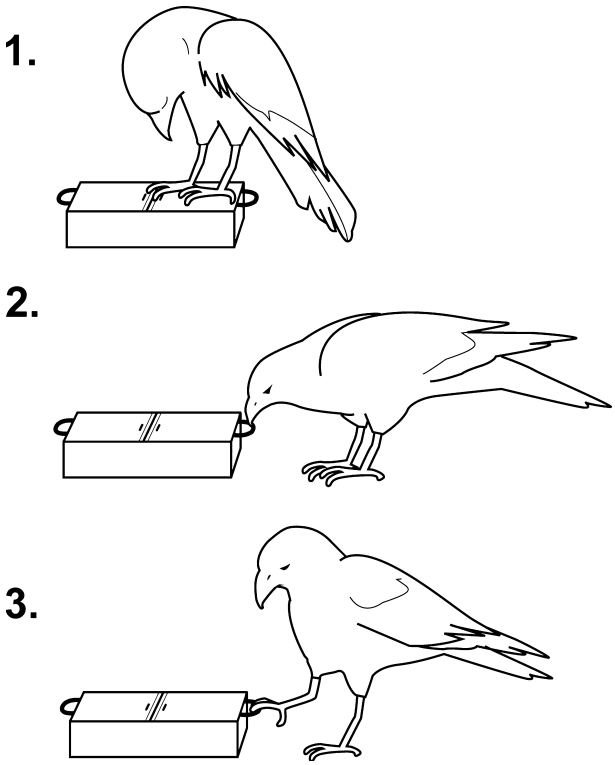

Fig. 2: Schematic drawing of the three opening techniques used by the control and observers individuals. See the text for details.

required similar amounts of time to open the experimental box and used the same technique: from the midpoint of the box, the demonstrators pecked the lids' edges in the central divider of the box, introducing the tomium into the interior rims of the lids and thus sliding the lids simultaneously to opposite sides and opening the box (Fig. 2.1).

Observer test phase

Twenty-four hours after the end of the observation phase, each observer was tested again, in isolation, with the closed Plexiglas box with food inside, during a session of 1500-s duration (D1). The variables reordered for each bird were latencies to approach, contact and open the box. We also recorded a description of the technique used by each bird to open the box and reach the food inside. Subsequently, all observers were given two additional test sessions (1500-s duration), one session per day (D2-D3), with the box to assess the persistence and performance of the opening behaviour across different session days. During these additional test sessions, we recorded the same variables as on D1. If an individual did not respond to the box during any of these session days the maximum value of 1501 s was recorded for each latency measurement (approach, contact and opening), for each experimental session.

Controls

The experimental procedure used for control birds was the same as that used for the observer group, except that control birds were not given an observation phase with a demonstrator. Thus, control birds were confronted with the opaque Plexiglas box during a first single session (D0) of 25-min duration, followed by a break of 11 d during which the control individuals were not presented with any task (during this time, they were provided with food once per day and water *ad libitum)*. After this period, each control bird was given a series of three additional experimental sessions of 25-min duration each, one session per day (D1-D3). We again recorded latencies to approach, contact and open the food box. When an individual was able to open the box and reach the food inside, we also recorded a description of the technique used.

Analysis

Because observers were allowed to see a demonstrator opening and feeding from the box after having had an opportunity to explore and learn about the test apparatus individually, we predicted that these birds would show an increase in their opening success from D0 to D1. This problem-solving improvement should be of a higher magnitude compared to control individuals, because this last birds group only had the chance to learn about the test apparatus individually and they did not have any visual clue about the reward hidden inside the box. Therefore, the effect of observing the behaviour of a demonstrator in the response to the operant box by adult and juveniles individuals was analysed using generalized linear mixed models (thereafter GLMM). These models were constructed including the interaction between age class (adults, juveniles), treatment (control, observer), and session day (D0, D1) as explanatory variables, and the behavioural responses – approach, contact, and opening latencies, as well as, opening success – for these 2 d session days, as response variables. Considering the non-independence of data between response variables during D0 and D1, the bird's identity was included as a random effect. The latencies registered in each session were converted to proportions, with respect to the maximum time session given to each

individual (latency/1500 s), and the opening success was modelled as a binary response (one success, 0 fail). A binomial error structure and logit link function was used for all response variables (Pinheiro & Bates 2000; Crawley 2007).

To examine whether adult and juvenile observers were differently influenced by the age of the demonstrator, we used a general lineal model (thereafter GLM) to analyse contact and opening latencies following the observation phase. The model included demonstrator and observer age as explanatory variables (two factors with two levels each), and contact and opening latencies as response variables (converted to proportions with respect to the total duration of the session). A binomial error structure and logit link function was used for both response variables (Crawley 2007).

Finally, variation in task solving performance by observer and control individuals was evaluated by comparing the latencies to approach, to contact and to open the test apparatus during three consecutive session days (from D1 to D3). The latency values were converted to proportions with respect to the total duration of the session (latency/1500 s). We used a GLMM with a binomial error structure and logit link function (Pinheiro & Bates 2000; Crawley 2007) to test the effects of two explanatory variables (session day [D1, D2, and D3] and age class) on latency values. As before, individual ID was included as a random effect to account for non-independence of data across session days.

Models fitting were visually assessed inspecting plots of standardized deviance residuals for each model. We assessed goodness of fit for all models and estimated the variance inflation factor ($\hat{c}$) as residual deviance divided by degrees of freedom (Burnham & Anderson 1998). We fitted GLMM using the glmmPQL function of the MASS package from R software, Version 2.7.0 (R Development Core Team 2008).

Results

First Exposure to the Operant Box (D0)

During D0, most control and observer individuals showed a variable degree of curiosity about the opaque closed box. In the observer group, 83% of the individuals (seven adults and eight juveniles) approached the box (Fig. 3) with a mean latency of 383.6 ± 213.6 s for adults and 200.8 ± 154.2 s for juveniles (Fig. 4). In the control group, 70% of the individuals (two adults and five juveniles) approached the box with a mean latency of 761.7 ± 426.2 for adults and 350.6 ± 231.3 s for juveniles (Fig. 4). Of the observers that approached the box during D0,

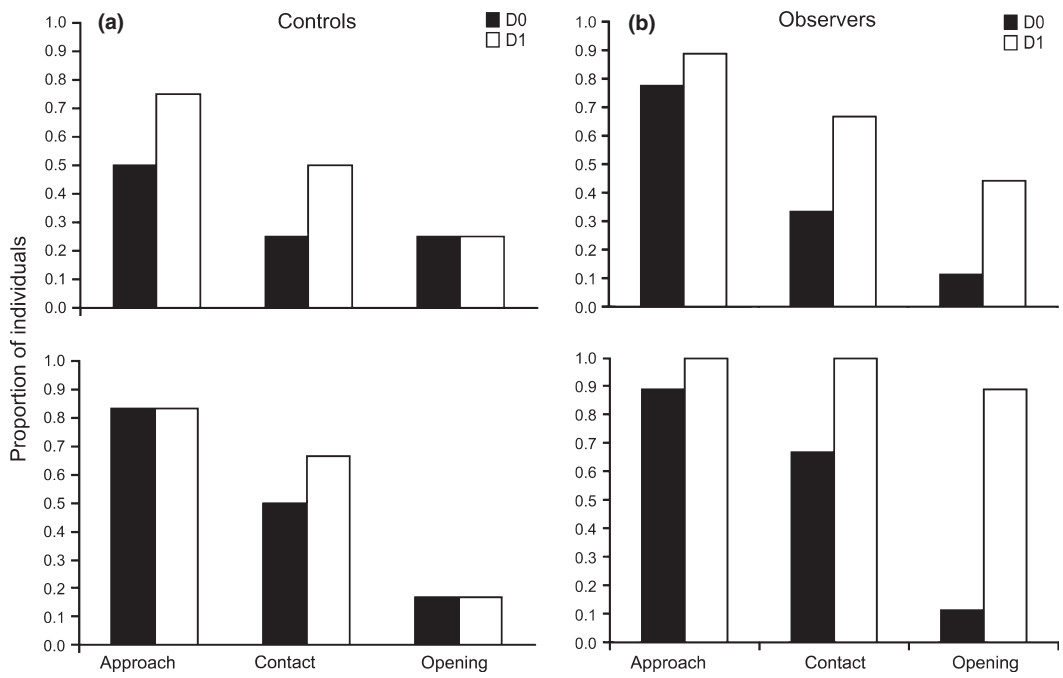

Fig. 3: Proportion of adults (a) and juveniles (b) in control and observer group that performed each of the three behaviour categories: approaching, contacting and opening the box, during D0 and D1.

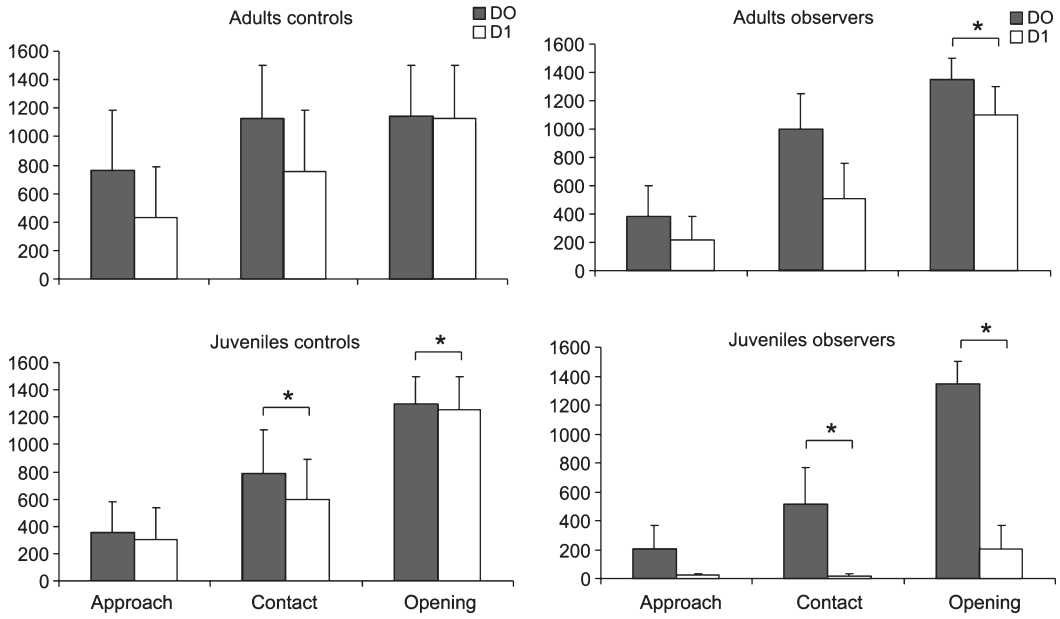

Fig. 4: Comparison between D0 and D1 in the latency values (means ± SE) showed by adult and juvenile individuals of the observers and controls group. The asterisks indicate statistically significant differences of $p < 0.05$.

60% (three adults, six juveniles) contacted the box at least once (Fig. 3). For these individuals, the mean contact latency was 1002.3 ± 248.8 s (n = 3) for adults and 517.4 ± 245.8 s (n = 7) for juveniles (Fig. 4). Only two individuals opened the box during the control session (Fig. 3): one juvenile reached the food inside the test apparatus after 109 s and one adult did it after 140 s. In the control group, 57% of the individuals that approached the box during D0 also contacted it (one adult and three juveniles), with a mean latency of 1131.1 s for the adult and 790.5 ± 318.4 for the juveniles (Fig. 4). As in the observer group, only two controls opened the box during D0 (1 adult after 135 s and 1 juvenile after 334 s). There were no differences between adult and juvenile controls in any of the behavioural variables registered during D0 (Table 2a). The same result was found in the case of the observer group. The GLMM also showed that there was not a significant difference during D0 in any of the behavioural variables between observer and control group, nor for adult individuals neither in juvenile birds (Table 2c).

Observation Phase

During the observation phase, all observers centred their attention on the demonstrator behaviour. The interaction between the demonstrator and the closed box, immediately after its presentation, usually caused the observer to approach the side of its cage next to that of the demonstrator. The observers typically walked backward and forward with apparent nervousness (i.e. plumage erection, vocalizations), always with its head oriented towards the demonstrator's location, clearly attracted to the demonstrator's interaction with the box. The observer's actions persisted until the demonstrator finished feeding from the box and occurred during all observation sessions. The demonstrators showed signs of tension (mainly feathers bristling), probably as a result of the displays and vocalization of the observers. Despite this, the demonstrators always continued to open and feed from the box. All demonstrators used the same opening technique (Fig 2.1) and opened the box after approximately the same period of time (<1 min).

Observer Test Phase

During D1, 94% of the observers (eight adults and nine juveniles) approached the Plexiglas box (Fig. 3). The values of the approach latencies (218.5 ± 161.9 s for adults, and 21.7 ± 8.3 s for juveniles, Fig. 4) during this session day were not statistically different with respect to D0 (Table 2b). Three of these birds (two adults, one juvenile) had not approached the box during the control session. In juvenile observers, the GLMM showed a significant effect of the observation of a demonstrator on the latency to contact the box (Table 2b). Adult

Table 2: Fixed factors contrasts resulted from generalized linear mixed models testing the effect of the interactions between (a) age classes (Adults-Juveniles), (b) session days (D0-D1) and (c) groups of individuals (control–observer) on four behavioral variables registered before and after the observation phase. In each model, individual identity (ID) was included as a random factor

	Approach latency			Contact latency			Opening latency			Opening success		
Fixed factors contrasts	*DF*	*t*	*p*	*DF*	*t*	*p*	*DF*	*t*	*p*	*DF*	*t*	*p*
a) Age (Adults vs. Juveniles)												
Controls D0	21	−1.06	0.299	21	−0.85	0.403	21	0.41	0.685	21	−0.26	0.795
Observers D0	21	−0.72	0.477	21	−1.71	0.103	21	−0.62	0.541	21	1.37	0.186
Controls D1	21	−0.17	0.868	21	−0.28	0.782	21	0.29	0.773	21	−0.26	0.795
Observers D1	21	−1.28	0.214	21	−2.55	0.019	21	−2.94	0.008	21	2.84	0.010
b) Session day (D0 vs. D1)												
Adults controls	24	−1.25	0.222	24	−1.79	0.086	24	−1.04	0.308	24	0.00	1.000
Juveniles controls	24	−1.02	0.316	24	−3.50	0.002	24	−13.24	0.000	24	0.00	1.000
Adults observers	24	−0.25	0.801	24	−1.13	0.268	24	−2.30	0.031	24	2.E+05	0.000
Juveniles observers	24	−1.40	0.173	24	−3.49	0.002	24	−19.98	0.000	24	2.E+05	0.000
c) Group (Controls vs. Observers)												
D0 Adults	21	−1.09	0.287	21	−0.38	0.707	21	1.12	0.274	21	−1.84	0.080
D0 juveniles	21	−0.54	0.592	21	−0.74	0.469	21	−0.67	0.512	21	0.91	0.374
D1 Adults	21	−0.61	0.551	21	−0.93	0.364	21	0.22	0.829	21	−0.55	0.586
D1 juveniles	21	−1.51	0.146	21	−2.80	0.011	21	−3.73	0.001	21	3.01	0.007

observers showed a similar decrease than juveniles in the contact latency on D1, but the effect was not statistically significant (Table 2b). On average, individuals contacted the box faster on D1 than on D0 (506.78 ± 248.3 s for adults, 19.4 ± 10 s for juveniles, Fig. 4), and the proportion of individuals that contacted the test apparatus increased from 50% on D0 to 83% on D1 (15 individuals: six adults, nine juveniles, Fig 3). The proportion of individuals that opened the operant box increased from 11% on D0 (two birds; one adult, one juvenile) to 67% on D1 (12 individuals; four adults, eight juveniles), with a mean opening latency of 1100.8 ± 201.3 s for adults and 205.8 ± 163 s for juveniles (Fig. 4). The GLMM revealed that in adult and juvenile birds there was a significant effect of the observation of a demonstrator on the latency to open the opaque box, though only in juveniles the opening success differed between D0 and D1 (Table 2b). Adults and juveniles observers differed significantly in the behavioural variables recorded on D1, excepting for the approach latencies. In overall, young observers seemed to be more influenced by the observation of a demonstrator, showing lower latency values and a higher opening success than adult birds on D1.

Control Birds

Only one additional control individual (one adult) approached the operant box during D1 that had not approached it on D0, whereas the number of individuals contacting the box increased from 4 to 6 (one adult and one juvenile). Of the individuals that did not succeed in opening the box on D0, none succeeded in opening the box on D1 (Fig. 3). The latencies to approach the box were lower compared to D0 (434.7 ± 356.8 for adults and 298.8 ± 240.7 for juveniles, Fig. 4), though the GLMM did not reveal a statistically significant difference between these sessions, for both adults and juveniles birds (Table 2b). In the adult group, all the rest of the behavioural variables showed no significant differences between D0 and D1 (Table 2b). Despite this, there was a tendency to decreased the time until the first box contact (757.7 ± 428.5 s, Fig. 4), and the only adult that opened the box during D0 showed a decrease in their opening latency from 135 s during D0 to 80 s during D1. In juveniles birds, the GLMM showed a significant difference in the latencies to contact and open the box between D0 and D1 (Table 2b). During D1, juvenile controls contacted the operant box with lower latencies (594.3 ± 292.8 s, Fig. 4) than D0, and the only juvenile that opened the box during D0 decreased their opening latency towards D1 (158 s). Regarding the age comparison, the GLMM evidenced a lack of statistically significant difference between adult and juvenile controls in all the behavioural variables registered during D1 (Table 2a).

Control vs. Observer Birds During D1

Overall, observer individuals outperformed control birds in solving the box-opening task during D1

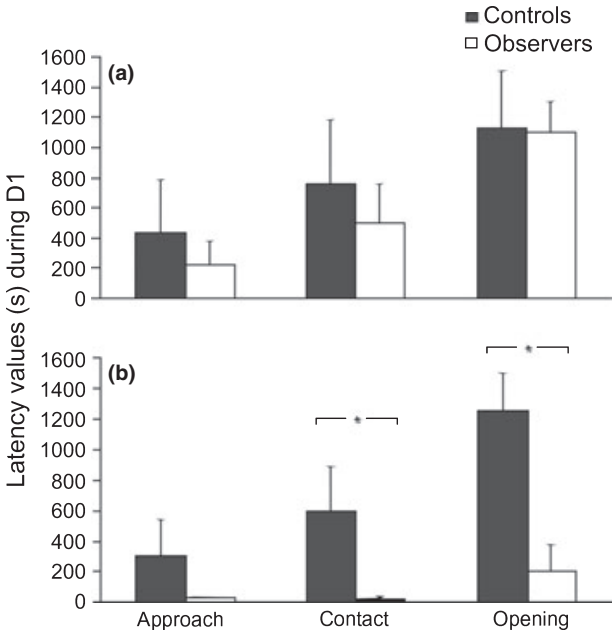

Fig. 5: Comparison between control and observers birds of the latency values (means ± SE) showed by adults (a) and juveniles (b) birds during D1. The asterisks indicate statistically significant differences of $p < 0.05$.

(Fig. 5). Approach latencies were lower in the observer group than in the control group, though the differences were not statistically significant in either age class (Table 2c). Juvenile observers showed lower contact and opening latencies and had a higher success in opening the opaque box than juvenile controls (Fig. 5, Table 2c). Similarly, adult observers contacted and opened the box faster than adult controls during D1, and showed a higher opening success during D1 (Fig. 5), though the effect did not reach the statistical level of significance (Table 2c).

Observer and Control Opening Techniques

Three principal opening techniques could be identified in the observer and control birds (Fig. 2): (1) from the midpoint of the box, pecking and introducing the tomium into the interior rims of the lids, thus pushing them simultaneously to opposite sides of the box; (2) from the lateral part of the box, pulling one of the lids outward by grasping the handle with the bill and (3) the same as 2, but by scraping the lid with the talons. The first technique was most frequently used by the observers (10 individuals) and is the one used by all demonstrators. Six observers used the second technique, and the remaining two observers opened the box with the third technique. All observers continued to use the same technique during subsequent trials. Of the two control individuals that successfully opened the box, one of them (an adult) used the first technique and the other (a juvenile) used the second technique. Both of these control birds used the same technique to open the box in all subsequent trials.

Effect of the Demonstrators' Age

The age of the demonstrators did not affect the observers' box-opening performance on D1: young and adult birds, which were confronted with juvenile demonstrators, did not differ significantly in their latencies to contact (GLM, $t = 0.755$, $p = 0.463$) and to open the box (GLM, $t = -0.044$, $p = 0.9652$) compared with those that observed adult demonstrators. Moreover, the interaction effect between the demonstrators' age and observers' age was statistically not significant in either response variables (GLM, contact: $t = -0.669$, $p = 0.514$; opening: $t = 0.530$, $p = 0.6045$).

Performance of Box-Opening Behaviour on Subsequent Days

Observers that successfully opened the Plexiglas box on D1 were also able to open it on the following session days (D2 and D3). Of those observer birds that did not open the box on D1, only two succeeded on D2 (one adult and one juvenile) and continued to be successful during the following sessions. The remaining four observers (all adults) did not open the box on any of the session days. With respect to the improvement in problem-solving ability across session days, the observer group showed similar approach and contact latencies from D1 to D3 (Table 3a), and there were no significant differences between age classes on any session day in either latencies (Table 3b). In contrast, opening latencies decreased across session days in the observer birds, particularly between D1 and subsequent session days (Table 3a). Moreover, the GLMM showed a difference in opening latencies between adult and juvenile observers, though this difference was only statistically significant on D1 (Table 3b), with juveniles opening the operant box more quickly than adult observers. Regarding control individuals, the GLMM revealed that none of the latencies analysed varied significantly among session days (Table 3a). Moreover, there were no differences between adult and juvenile controls in these behavioural variables on any session day (Table 3b).

Table 3: Results from generalized linear mixed models for observer and control individuals comparing the approach, contact and opening latency from D1 to D3 (a), and between adults and juveniles during each session day (b)

Group	Contrast: age classes	Approach z	Approach p	Contact z	Contact p	Opening z	Opening p
(a)							
Controls	D1	−0.23	0.821	−0.38	0.702	0.28	0.781
	D2	−1.01	0.315	0.43	0.666	0.17	0.860
	D3	−0.49	0.623	−0.04	0.969	0.16	0.867
Observers	D1	−0.34	0.706	−0.45	0.652	−3.01	0.002
	D2	−0.77	0.493	−0.49	0.622	−1.43	0.152
	D3	−0.53	0.594	−0.33	0.738	−1.23	0.218
Group	**Contrasts: session days**	**Approach z**	**Approach p**	**Contact z**	**Contact p**	**Opening z**	**Opening p**
(b)							
Controls	D1 vs. D2	0.97	0.329	0.01	0.999	0.13	0.895
	D2 vs. D3	0.61	0.545	−0.65	0.513	0.12	0.905
	D1 vs. D3	0.95	0.335	−0.02	0.987	0.13	0.901
Observers	D1 vs. D2	1.24	0.216	0.78	0.432	−2.34	0.019
	D2 vs. D3	0.56	0.571	0.54	0.588	−0.07	0.941
	D1 vs. D3	0.72	0.468	0.23	0.821	−2.35	0.018

Discussion

In this study, we evaluated social learning ability, which was evaluated in the Neotropical Caracara *Milvago chimango*. We tested whether the actions of a conspecific 'demonstrator' influenced the ability of an 'observer' to open an opaque Plexiglas box containing food, and we investigated potential effects of the age of observers and demonstrators. Four major conclusions can be drawn from the results: (1) those individuals that could see a demonstrator opening and feeding from the opaque box showed a better performance in solving this operant task compared to control individuals, which did not have previous visual contact with a conspecific demonstrator, (2) this learned ability persisted across different session days, (3) social learning performance was in general better in young birds than in adults individuals and (4) the age of the demonstrator did not influence the probability of social learning in either adult or juvenile observers.

Direct or indirect social interaction may influence the acquisition of new information, the direction of behaviour towards a novel resource or the performance of a novel pattern of behaviour (Nicol 1995). If the new behaviour is retained by the naive individual (observer) in the subsequent absence of the model (demonstrator), then the social process that facilitated the acquisition of the new behaviour is often described as social learning (Nicol 1995). In the present study, the observation of a model interacting with and opening the Plexiglas box to reach the food hidden inside affected both the observers' latency to contact the box and the success to open it. The number of observers which contacted and opened the box increased after the observation phase and the time it took them to contact and open the box decreased significantly. Additionally, those birds which solved the task on D1 were also successful during subsequent sessions with the test apparatus, suggesting a temporal persistence of the acquired behaviour across session days. By contrast, in the control group, there were no additional individuals that succeeded in opening the test apparatus after D0. Furthermore, on D1, this group exhibited a considerably higher contact and opening latencies, as well as, a lower opening success compared to individuals in the observer group.

Although the experimental procedure used in this work was not designed to discriminate among the possible mechanisms of social learning, it is unlikely to consider that the observer individuals learned to open the box by some form of imitation. This is because not all observers matched the motor actions of the demonstrators: while all of the demonstrators opened the box by pecking the midpoint of the interior rims, some of the observers used a different technique to reach the reward (behaviours topographically dissimilar to that performed by the model). This result suggests that a non-imitative form of social learning was probably involved (i.e. stimulus enhancement, observational conditioning or emulation).

Experimental studies have showed that factors such as sex, age, dominance rank and motivation may cause differences between individuals in the likelihood of both learning and transmitting adaptive information (e.g. Nicol & Pope 1999; Reader & Laland 2000; Nicol 2004; Pongrácz et al. 2008). Regarding age, it could be argued that young animals, for which many potential foods and feeding places are unfamiliar, may be particularly motivated to and benefit from attending and copying the behaviour of others. By learning from more experienced individuals, naïve juveniles may reduce the need for time-consuming and costly trial-and-error learning (Galef 1993). For example, some studies have revealed that younger animals are more likely to incorporate new behaviours into their repertoires, as is the case of pine cone opening in black rats (Terkel 1995) and food palatability in domestic fowls

(Nicol 2004). Moreover, adult animals seem to be more resistant to changing their behaviour as a result of observation (Miklósi 1999). In support of these findings, young birds in this work outperformed adults in the box-opening task after being confronted with a conspecific demonstrator. During the first session after the observation phase, almost all juveniles opened the Plexiglas box, whereas only half of the adults were able to do it. In addition, opening latencies showed differences between age classes: juveniles were faster than adults at opening the test apparatus. It is well known that the fear of or the aversion to novel situations (neophobia) limits explorative behaviour and may constrain exploitation of novel food opportunities, learning and innovation (Kotrschal et al. 2001; Seferta et al. 2001; Greenberg 2003; Reader & Laland 2003). It might therefore be expected that the level of neophobia would affect the observers' response to the opaque container in this study. In fact, the chimangos did not show clear aversion to the box, even when they were confronted with it for the first time. Moreover, adults and juveniles did not differ markedly in the latency to contact the experimental box in the first session after the observation phase. Consequently, the difference in task solving performance cannot be attributed to different levels of neophobia to the box. Two alternatives might be proposed to explain this age difference. First, it could be argued that the majority of both juveniles and adults in this study learned to associate the box with a food reward by observing the behaviour of a model, though only juveniles were capable of learning the technique or motor actions needed to open the box (i.e. directing the major pecking effort towards the medial area of the box). However, this is unlikely because some juveniles were able to open the box using a different technique from the one used by their demonstrators. Second, it is possible that adult and juvenile observers learned only the association between the box and the food reward and not the technique needed to open it. The difference in opening latency and success was probably because of the fact that young birds are more persistent and better performers in problem-solving tasks compared to older birds. In support of this, a related study of individual learning and problem-solving ability of the same species found that juveniles are more proficient than adults at solving a novel feeding problem (Biondi et al. 2010).

According to Lefebvre & Palameta (1988) and Coussi-Korbel & Fragaszy (1995), the occurrence of social learning is more likely to reflect a species' ecology and social organization than its phylogeny. The effect of social dynamics on modulating social learning is of importance in understanding when and how social learning will occur (Galef & Laland 2005). Implicit in this idea is the notion that directed social learning is likely to occur in groups where social dynamics affect the salience of various individuals for each other, for instance in a despotic society. On the other hand, in an egalitarian (tolerant) social system, socially acquired information spreads more equally across all group members because of closer proximity and more tolerant relationships among individuals (Coussi-Korbel & Fragaszy 1995). This would also suggest that the identity of the demonstrator might influence observational learning less in egalitarian than in despotic societies (Range & Huber 2007). Therefore, to detect directed social learning one must demonstrate that particular individuals acquire more information from certain individuals than from others. In raptors, the age class and body size are frequently related to the hierarchical rank in the majority of the gregarious species (Newton 1979). Consequently, in this study, we considered the demonstrator's age to be a possible factor involved in the variation in social learning ability. However, our results did not demonstrate a significant effect of this demonstrator's characteristic on the observer problem-solving success. Others factors, such as the demonstrator's sex or dominance rank (Coussi-Korbel & Fragaszy 1995) may influence the social learning ability in *M. Chimango*. Our results also suggest that differences in performance registered among observers were most likely due to both the observers' age and the individual variation in problem-solving ability. Hitherto, the social dynamics of *M. chimango* have not been well studied yet, so it cannot be accurately placed within the despotic-egalitarian continuum. Nevertheless, this raptor usually congregates in large feeding groups of all age classes when food concentrations are discovered (i.e. insects or carrion), as well as for resting and breeding (Fraga & Salvador 1986; Fergusson-Lees & Christie 2001; Biondi et al. 2005). Therefore, it is likely that the level of tolerance towards the close presence of conspecific is increased under these circumstances, thus enhancing the probability that some behavioural patterns can be socially transmitted through all members of a group.

Finally, it is worth noting that observers and controls, regardless of their age class, showed a notable variation in their response to the novel container, not only after being faced to a demonstrator in the case of observer birds but also during D0, when all

individuals had to deal with the test apparatus for first time. To this respect, two individuals in each group opened the box after its first presentation by the researcher during the D0. Although the individuals that opened the box without the influence of a demonstrator represented clearly a minority of the birds in our study, this surprising result might be evidence of the highly explorative behaviour and innovative ability of this raptor species, at least of some individuals. Under natural conditions, this behavioural flexibility may be of great importance for a generalist and opportunistic species (Lefebvre et al. 1997; Laland & Reader 1999; Greenberg 2003; Lefebvre & Bolhuis 2003), like *M. chimango*, which must deal with changing environment and temporally and spatially heterogeneous feeding opportunities.

In conclusion, this study showed that *M. chimango* can improve the acquisition of novel information about a food resource observing the behaviour of a conspecific demonstrator, an ability that was particularly conspicuous in young individuals. The benefits of social learning to *M. chimango* include an improved ability to find and use food resources in novel or modified habitats (i.e. urban areas). This is especially true for post-fledging juveniles which, like in other juvenile raptors (Newton 1979), must disperse from the natal area to novel territories about which they do not have any information. Thus, the gregarious habits exhibited by *M. chimango*, along with their ability to acquire novel behaviours via individual learning (Biondi et al. 2008, 2010), are likely to influence social learning opportunities in natural conditions. These characteristics allow some adaptive behavioural patterns to be socially transmitted, and it could represent one of the interviniente factors in the ecological success of this raptor.

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