

Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*)

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Abstract Animal innovations have far-reaching ecological and evolutionary consequences. The occurrence and persistence of an innovation require several processes, including exploration, social and asocial learning, and low neophobia. In addition, the identity of the innovator may determine how these new behaviours are socially transmitted. Taking into account inter-individual and age differences, we investigated three correlates of animal innovation: object exploration, neophobia level and novel problem-solving ability in an opportunistic generalist raptor, the Chimango Caracara (*Milvago chimango*). Eighteen individuals (7 adults and 11 juveniles) were caught during the non-breeding period and housed in individual cages in outdoor aviaries. Each bird was given three tests: exploration, neophobia and problem-solving. Individuals differed in their response to novel situations both within and between age groups. Most of the juveniles were more explorative and had a lower neophobic response to a

strange object than adult birds, but both age groups were able to solve a novel problem when given a food reward. In juveniles, neophobia level and problem-solving performance were inversely related; however, we found no relationship between these behaviours in adults. Exploration did not correlate with neophobia or problem-solving ability for either age group. This research is one of the few studies exploring the inter-individual and age differences in behavioural innovation and their correlates in a bird of prey. The explorative tendency, low neophobia and ability to innovate showed by *M. chimango* may be advantageous for this generalist and opportunistic raptor and might be some of the factors underlying its ecological success.

Keywords *Milvago chimango* · Neophobia · Exploration · Problem-solving ability · Innovation · Age · Urbanization

Introduction

Animal innovation is a process that results in new or modified learned behaviour, introducing novel behavioural variants into a population's repertoire (Reader and Laland 2003; see Ramsey et al. (2007) for a discussion of the definition of innovation). These novel behaviours allow individuals to exploit newly available, previously unused, or familiar resources in a different way (Lefebvre et al. 1997; Reader and Laland 2001; Reader 2003; Greenberg 2003). Innovations are crucial for the creation of new niches and may have correspondingly important evolutionary consequences (Wyles et al. 1983; Nicolakakis et al. 2003; Reader and Laland 2003). They are important sources of behavioural plasticity in animals and vital for the survival of generalist and opportunistic species as well as for individuals that are colonizing a new habitat or facing competition for

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resources in a species-typical habitat (Lefebvre et al. 1997, Laland and Reader 1999a; Greenberg 2003, Lefebvre and Bolhuis 2003; Sol 2003).

An approach to the study of animal innovation is the analysis of those behavioural processes that promote the acquisition and transmission of innovative behaviours (Greenberg 2003), such as spatial and object exploration, social and asocial learning, and low neophobia (Reader 2003). Indeed, comparative studies in birds, fish and primates have shown a positive association between these processes and innovation rate. Additionally, a correlation between innovation and other cognitive abilities such as problem-solving performance and tool use has been found. Innovativeness is also positively correlated with relative brain size in both birds and primates (e.g. Lefebvre et al. 1997, 1998, 2001; Webster and Lefebvre 2001; Lefebvre and Bolhuis 2003; Reader 2003; Lefebvre and Bolhuis 2003), which suggests that cognitive capacity can facilitate (or limit) the ability of a species to innovate (Overington et al. 2009).

Neophobia—the level of aversion to novel situations—and exploration are integrally related to ecological plasticity, opportunism and innovative behaviour (Greenberg and Mettke-Hofmann 2001). For example, the neophobia level in birds influences the response towards new feeding situations (Greenberg 1983, 1984, 2003), and hence the ability to assess and learn about new environmental information (Heinrich 1995, Schwagmeyer 1995, Mettke-Hofmann et al. 2006). Exploration and neophobia have been regarded as two independent responses to a novel stimulus (Russell 1973). This view is consistent with the ambivalent approach-withdrawal responses to a new situation observed in some of the most innovative taxa, such as corvids and psittacines (Greenberg 2003). In line with these observations, it has been hypothesized that exploration and neophobia are shaped by different selective forces (Greenberg and Mettke-Hofmann 2001). Exploration should be favoured when the gathering of information about novel situations will yield the greatest benefit, i.e., circumstances of habitat complexity, hidden and/or unpredictable resources (Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann et al. 2002, 2005). In contrast, neophobia is more sensitive to the cost function, and it is mainly related to the degree of ecological specialization of the species and the level of danger from predation and poisonous prey (Greenberg and Mettke-Hofmann 2001). The resulting behaviour is a dynamic balance between the two response functions associated with these behaviours (Greenberg 2003).

The innovator's identity may be an important determinant of the social transmission of new behaviours. However, virtually nothing is known about which individuals invent new behavioural patterns and which ecological variables influence innovation (Laland and Reader 1999a;

Reader and Laland 2001). It is not yet clear whether animal innovation should be regarded as temperament differences (associated with particularly clever or creative individuals), as a state-dependent variable (for example, foraging innovation may be driven by hunger, reproductive state or age and dominance status) or as a result of exposure to pertinent ecological stimuli (for instance, a sudden change in the environment). Observations made on wild animals, as well as experiments performed under controlled conditions, suggest that innovators often differ from the rest of the group in some characteristics, such as age, sex or dominance rank (e.g. Katzir 1982a, 1982b; Kummer and Goodall 1985; Laland and Reader 1999a, 1999b; Reader and Laland 2001; Pfeffer et al. 2002; Kendal et al. 2005; Gajdon et al. 2006; Bouchard et al. 2007; Boogert et al. 2008). In juvenile birds, low neophobia, active play and exploration are frequently observed (Heinrich 1995, Greenberg 2003). This willingness to interact with novel situations helps young birds to acquire new behaviours more easily than adults (see Gajdon 2007).

Birds of prey (Falconiformes) possess proportionately large brains and are highly innovative and opportunistic species (Nicolakakis and Lefebvre 2000; Lefebvre et al. 2001; Nicolakakis et al. 2003); however, few studies have evaluated innovative ability and correlated behaviours in raptors (Schaden 1993; Beissinger et al. 1994, Biondi et al. 2008). The Chimango Caracara (*Milvago chimango*) is a small (250–300 g) Neotropical caracara that lives in a wide range of habitats. It is usually associated with suburban and urban settings, but also inhabits natural areas (White et al. 1994; Morrison and Phillips 2000; Biondi et al. 2005). This species is gregarious (feeding, roosting and nesting in aggregations or colonies) and highly opportunistic, preying on arthropods, small mammals, birds, reptiles, amphibians and carrion. It also kleptoparasitizes other birds (Garcia et al. unpublished data) and takes advantage of agricultural practices and discards from other human activities, such as fishing and camping (Cabezas and Schlatter 1987; Biondi et al. 2005). In urban settings, it mainly feeds on urban prey and garbage (White et al. 1994). Accordingly, some individuals have learned to open bins and bags to feed from human rubbish (LB, pers. obs.). The use of rubbish bins to access food has been described in several bird and mammal species; for instance, keas (*Nestor notabilis*) in New Zealand open rubbish bin lids with their bills to obtain food scraps, a highly innovative behaviour (Gajdon et al. 2006; Huber and Gajdon 2006). Similarly, the use of rubbish bins to obtain food may demonstrate an adaptive innovation by *M. chimango* that has facilitated its invasion of urban settings.

A recent study showed that *M. chimango* wild-caught juveniles are able to solve novel feeding problems in captivity (Biondi et al. 2008). This attribute probably underlies

their ecological plasticity in terms of habitat occupation and feeding behaviour. The aim of this study was a more complete evaluation of innovative behaviour in adult and juvenile individuals of *M. chimango*. Taking into account the inter-individual and age differences, we focused on three behavioural correlates of innovation: object exploration, object neophobia and novel problem-solving ability. Since cognitive traits are known to co-vary with responses to novelty, we predicted that novel problem-solving ability would be correlated with explorative behaviour, as well as with neophobia level. In particular, we expected a negative relationship between neophobia and problem-solving ability and a positive relationship between explorative behaviour and problem-solving ability. Finally, since age can influence the frequency with which birds investigate novel situations, we predicted that young birds should be more explorative, less neophobic and more successful in problem-solving tests than adults.

Methods

Seven adult birds (over 2 years old) and eleven juveniles (under 1 year old) were caught with baited walk-in traps (Bloom 1987) in a suburban area near Mar de Cobo village (Buenos Aires Province, Argentina) between March and August (non-breeding period) of 2006–2007. Plumage colour (mainly of rectrices), tarsus colour and moult stage were used to determine age (see White et al. 1994; Ferguson-Lees and Christie 2001). Housing and care conditions followed Bloom (1987) and Aprile and Bertonatti (1996). Birds were identified with leg bands and housed in individual cages (1.5, 1.5, 1.3 m³) in outdoor aviaries. The cages were visually isolated from one another by a black synthetic fabric, thus ensuring that the individuals performed on their own, without social motivation. To become habituated to captivity, birds were given a 1 week period during which they fed from a dish containing beef and chicken meat and drank ad libitum. Each subject was tested for exploration, neophobia and problem-solving, in that order, for three consecutive session days. During all tests, the subjects were video-recorded for later analysis of behavioural variables. Values are presented as mean \pm SE, and latency values are shown in minutes. All data were checked for homogeneity of variance using Levene's test, as well as for normality with Kolmogorov–Smirnov test. Non-parametric data were log-transformed [$\log_{10}(x + 1)$] to allow parametric statistical analysis or analysed with non-parametric statistical tests if transformation was not possible. The period of captivity was no longer than 2 weeks and all individuals were released at the capture sites at the end of the experiments.

Exploration test

Test subjects were presented with a set of objects without food present, in order to measure their intrinsic attractiveness. One hour before the trial, all birds were fed with the same amount of meat (50 g). They were then presented with six objects of two types: three natural objects (a dry starfish, a snail shell and a walnut) and three non-natural objects (a red cigarette box, a yellow plastic container [8 \times 5 cm] and a black plastic bag closed and filled with a load [10 \times 7 cm]). The objects were randomly arranged with 15 cm between them. Each bird was given 15 min to explore the objects during a single experimental session. We recorded the following data: (1) approach latency, measured as the time elapsed from the beginning of the trial to the time the individual approached the objects (within 10 cm); (2) contact latency, measured as the time elapsed from approaching within 10 cm to the time of first tactile contact with an object (with either the bill or feet); (3) the type and number of objects contacted and (4) the total exploration time for each individual. Explorative behaviour was considered to have ceased when the individual returned to its perch and did not visit the objects again during the experimental session. If an individual returned to its perch but visited the objects again during the 15-min experimental session, the additional exploration time was added to the previously recorded total exploration time. We compared approach and contact latencies for adults and juveniles using one-way ANOVAs. General linear models (GLMs) were used to investigate the effect of two fixed factor explanatory variables (object type and age) on the number of objects contacted and on the total exploration time. Since each individual contributed two data points (one for non-natural and one for natural objects), individual identity was included in both models as a random factor nested within age in order to avoid pseudo-replication. We also used GLMs to analyse the relationships among total exploration time (response variable), the number of objects explored (continuous explanatory variable) and age group (categorical explanatory variable).

Neophobia test

Subjects were tested for their latency to feed in trials with a novel object or no novel object next to a food dish (following Greenberg 1984). First, we presented test subjects with a dish containing meat. After the bird approached and consumed the first piece of meat (approximately 5 g), a researcher interrupted the feeding, approached the bird and placed a novel object next to the dish with the rest of the food. Each individual was then given 15 min to return to the dish. If a bird did not eat within this time, we recorded a 15-min maximum latency. The novel object used in this test

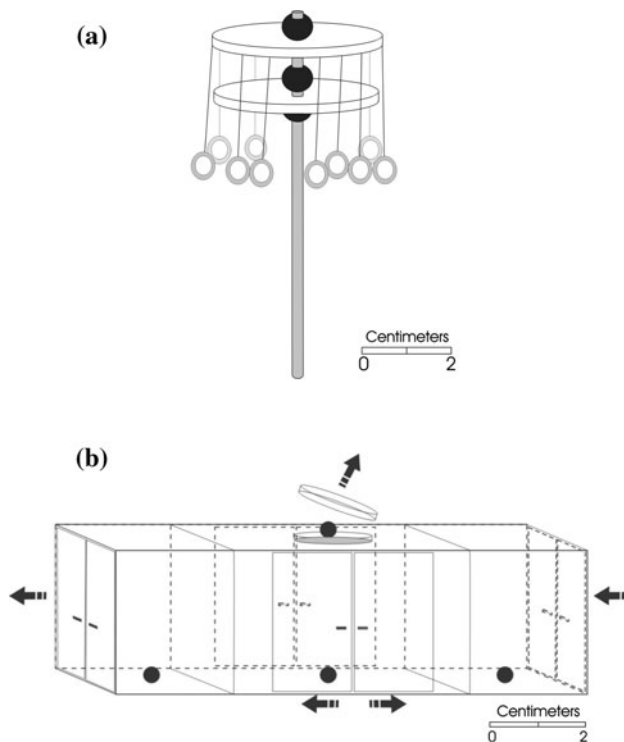


Fig. 1 **a** Novel object used in the neophobia test, **b** Diagram of the clear Plexiglas box used for the problem-solving test. Black dots represent the pieces of meat given to the subjects in each experimental test, and the arrows indicate the principal movement direction necessary to open each box lid

was a vertical copper-coloured stick (length: 20 cm) that supported two silver-coloured circular plates (diameter: 10 cm) (Fig. 1a). Three shiny blue balls were attached to the stick and several orange cardboard hoops dangled from the upper plate, presenting a colourful and non-natural object with moving parts. We predicted that this object should elicit an aversive response, since it is different in appearance from anything that the subjects could encounter in the wild. A GLM was used to analyse the effect of age group (adult vs. juvenile) and treatment (presence vs. absence of the novel object) on the latency to feed from the dish. Individual identity was included as a random factor nested within age group.

Problem-solving test

Test subjects were presented with a Plexiglas box filled with small pieces of beef. We used Webster and Lefebvre's (2001) design modified by Biondi et al. (2008) to make it suitable for *M. chimango*. The box has four isolated sections containing pieces of food. Each section can be opened by lifting, pushing, pulling or sliding the lids, respectively (Fig. 1b). In order to habituate the subjects to the experimental apparatus before the test, we first presented the box with all the lids open and the food accessible (day 0: control)

For five consecutive days, each bird was presented with a closed box loaded with food for one 25-min trial per day. During each trial, we recorded latency to first approach (at least 10 cm from the box), latency to first contact with the box and latency to first consumption (measured as the time elapsed from first contact with the box to access to the food). If the individual did not approach, contact or open the box within the experimental session, we recorded 25-min latency for each activity (approaching, contacting and feeding). We also recorded the number of attempts to open the box and the total number of lids opened by each individual. An "attempt" was defined as the action of picking and/or grasping one section of the box in a persistent manner. When the subject stopped making contact with the box for at least 5 s, the attempt was regarded as finished. To examine the variation in the three latency measures (approach, contact and consumption) and number of lids opened across session days, data were analysed using GLMs with age (categorical) and day (continuous) as explanatory variables. We also used a GLM to examine the relationship between lids opened on day one and the latency to first opening during that session day. The model included number of lids opened as response variable, as well as age (categorical) and feeding latencies (continuous) as explanatory variables.

Results

Exploration test

Fifteen of the eighteen test subjects touched and handled at least one object. From the three adult birds that did not explore any object, two stayed in their perches during the 15-min experimental session, and the third approached the objects but returned to its perch immediately after examining the objects for a few seconds.

Approach latency ranged from 0.02 to 1.94 min (excluding those individuals that did not respond) and did not differ between juvenile and adult birds ($F_{1,16} = 1.354$, $P = 0.261$). However, juveniles had significantly lower contact latencies than adults ($F_{1,16} = 8.42$, $P = 0.0104$) and investigated more objects (GLM: $F_{1,16} = 15.69$, $P < 0.001$; juvenile range: 2–5 objects, adult range: 0–3 objects) (Fig. 2). Object type (natural vs. non-natural) did not significantly affect the number of objects contacted (GLM: $F_{1,16} = 0.98$, $P = 0.34$), though there was a significant interaction between age and object type ($F_{1,16} = 5.16$, $P = 0.037$). Within age groups, a post hoc Newman–Keuls (SNK) test revealed that whereas adults did not differ in the type of objects explored ($P = 0.378$), juveniles explored more natural than non-natural objects ($P = 0.034$). Juveniles also explored for a significantly longer total time than adults

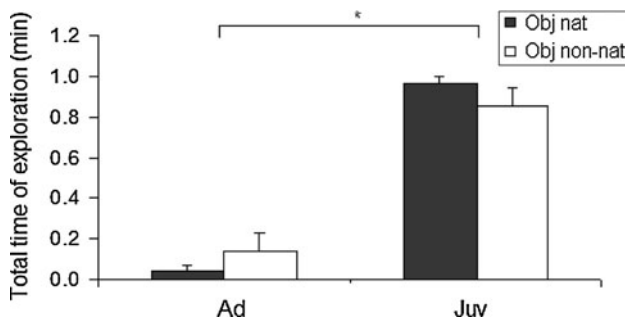


Fig. 2 Mean \pm SE total time of exploration devoted to natural (dry starfish, snail shell, walnut) and non-natural (red cigarette box, a yellow plastic recipient, a polyethylene black bag) objects by adults and juveniles of *M. chimango*. (*) $P < 0.001$

(GLM: $F_{1,16} = 12.729$, $P = 0.002$). Object type and its interaction with age did not have a significant effect on exploration time (GLM: $F_{1,16} = 0.012$, $P = 0.91$; $F_{1,16} = 0.31$, $P = 0.57$, respectively) (Fig. 2).

Overall, the total number of objects explored correlated with the total time of exploration (overall model: $R^2 = 0.72$, $F_{3,14} = 15.45$, $P < 0.001$). The number of objects contacted by each bird varied positively with exploration time ($F_{1,14} = 11.86$, $P = 0.004$; Fig. 3) and age group ($F_{1,14} = 12.55$, $P = 0.003$). The interaction between age and exploration time also showed a statistically significant effect ($F_{1,14} = 6.15$, $P = 0.026$). These results indicate that, in general, individuals that spent more time exploring also contacted and manipulated the largest number of different objects (Fig. 3).

Neophobia test

When the feeding dish was presented alone (control), all individuals approached and fed from it; when a novel object was added, all birds returned to feed except one

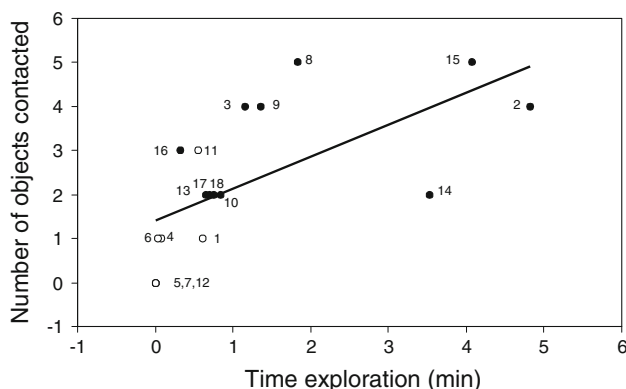


Fig. 3 Relation between exploration time and number of different objects explored by adults and juveniles of *M. chimango*. The black and white dots represent juvenile and adult individuals, respectively. Numbers indicate the identity of each bird

adult, which did not approach the dish during the 15-min experimental session. Behavioural responses to the novel object mainly consisted of erecting the neck feathers, approaching the dish with short backwards hops and runs ('jumping jacks' behaviour) and then quickly taking the meat out the dish and moving away from the object before eating.

There was a significant effect of treatment (with and without a novel object close to the food dish) on latency to food consumption (GLM: $F_{1,16} = 18.32$, $P < 0.001$). Individuals (within age group) ($F_{16,16} = 2.65$, $P = 0.029$) and age ($F_{1,16} = 8.13$, $P = 0.01$) showed significant effects on the latency to feed. The interaction between age and treatment was not significant ($F_{1,16} = 1.37$, $P = 0.25$). Latency to feed was higher in novel object trials (1.18 ± 0.44 min; 4.97 ± 2.28 min, juveniles and adults, respectively) than in control trial situations (0.20 ± 0.04 min; 0.67 ± 0.29 min, juveniles and adults, respectively) This pattern was more pronounced in certain individuals within each age group (Fig. 4).

Problem-solving test

All birds reached the food from at least one section of the experimental box during the control session (D0), except for one adult that did not approach the test apparatus during that session. The mean time to approach and contact the box during D0 was 5.50 ± 3.70 min for adults, 0.31 ± 0.08 min for juveniles and 5.87 ± 3.76 min for adults, 1.55 ± 0.88 min for juveniles, respectively. The mean latency to first food consumption from the open box was 3.62 ± 3.56 min for adults and 0.48 ± 0.28 min for juveniles. These latencies did not differ significantly between age groups (one-way ANOVA, approach:

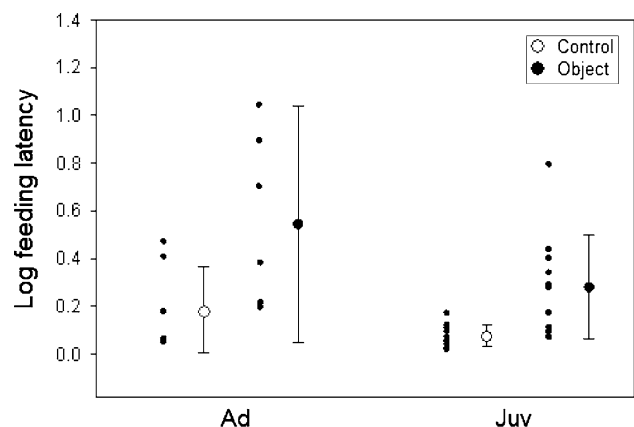


Fig. 4 Latencies to consumption with and without the presence of a novel object showed by *M. chimango* individuals during neophobia test. The dots with bars are mean \pm SE and points represent the individual date dispersion

$F_{1,16} = 2.84$, $P = 0.111$; contact: $F_{1,16} = 0.78$, $P = 0.390$; consumption: $F_{1,16} = 0.33$, $P = 0.575$).

When presented with the closed box, birds varied in their ability to solve the novel feeding problem. Over the five consecutive session days, performance improved and response variability decreased among individuals (Fig. 5). For each successful opening, individuals used either their legs or beak to manipulate the box handles and lid edges to open the box. The average time to approach the box ranged from 3.10 ± 2.12 min (adults) and 0.64 ± 0.41 min (juveniles) on D1 to 0.22 ± 0.08 min (adults) and 0.18 ± 0.05 min (juveniles) on D5. The average time to contact the box ranged from 4.32 ± 2.44 min for adults and 1.11 ± 0.46 for juveniles (D1) to 0.36 ± 0.08 min for adults and 0.25 ± 0.05 for juveniles (D5). Neither latency showed a statistically significant variation among session days (GLM, approach: $F_{1,86} = 3.54$, $P = 0.065$; contact: $F_{1,86} = 4.1307$, $P = 0.0501$), and age did not affect approach and contact latencies during closed-lid sessions (GLM,

approach: $F_{1,86} = 0.71$, $P = 0.405$; contact: $F_{1,86} = 1.457$, $P = 0.236$).

Latency to first box opening varied significantly among session days (GLM, $F_{1,86} = 15.41$, $P < 0.001$) and between age groups (GLM, $F_{1,86} = 5.08$, $P = 0.026$). However, there was no significant interaction between age and session day (age \times day: $F_{1,86} = 1.02$, $P = 0.315$). Similarly, the total number of lids opened by each bird increased linearly over time (GLM, $F_{1,86} = 5.74$, $P = 0.018$), and the two age groups differed significantly in the total number of lids opened (GLM, $F_{1,86} = 4.58$, $P = 0.035$). Over the course of the five session days, individuals opened more lids and were able to access the food more quickly. In the first experimental session (D1), 15 out of 18 individuals (83%) succeeded in reaching at least one section of the test apparatus; five of these (28%; four juveniles, one adult) opened all four box lids. In the last experimental session (D5), all individuals opened at least one lid, and nine birds (50%; seven juveniles and two adults) opened all four lids.

The total number of lids opened by the subjects during D1 was significantly predicted by the latency to first opening the box during that session day (GLM, overall $R^2 = 0.71$, $F_{1,14} = 30.41$, $P < 0.0001$). Age and its interaction with opening latency did not show significant effects (age: $F_{1,14} = 2.26$, $P = 0.154$; age \times opening latency: $F_{1,14} = 0.43$, $P = 0.521$). Individuals that opened lids more quickly (lower latencies) also opened more lids during this experimental session (Fig. 6).

Lid opening ‘efficiency’ for each individual was calculated as the number of attempts divided by the number of lids opened on each session (attempts/lid opened). A GLM was used to analyse variation in this rate over the five session days and between age groups. We found no significant variation in efficiency across session days or between adults and juveniles (GLM, days: $F_{1,86} = 1.29$, $P = 0.258$; age:

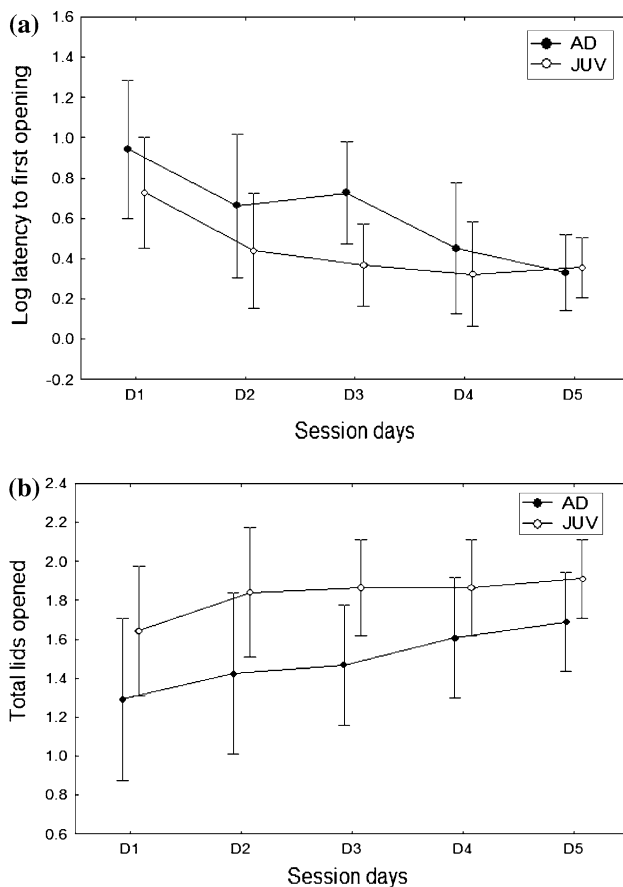


Fig. 5 : Results of the problem-solving test in *M. chimango*. **a** Time elapsed before solving the experimental box for first time (latencies to open the first lid), and **b** Total number of lids opened, during five subsequent session days exhibited by adult and juvenile birds. Day 0: control (lids open). Means are shown and vertical bars denote 0.95% confidence intervals

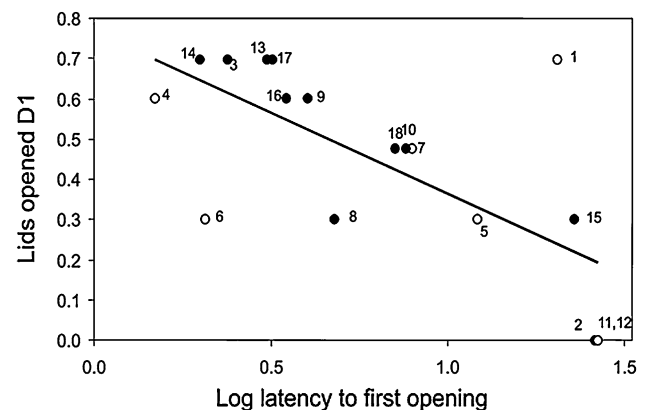


Fig. 6 Relation between latency to first lid opening during D1 and total number of lids opened on that session day during the problem-solving test by juvenile (black dots) and adult (white dots) individuals of *M. chimango*. Numbers identify each individual

$F_{1,86} = 0.32$, $P = 0.638$). Juveniles and adults were similarly successful in opening the box, though juveniles made more attempts and therefore opened more lids than adults.

We used a GLM to evaluate the predictive value of neophobia level and exploratory behaviour on the ability to solve the novel feeding task. Neophobia level (defined as the time difference between the latency to feed near the novel object and the control latency), total exploration time and age group were entered in the model as explanatory variables; the total number of lids opened during D1 was the response variable. Neither neophobia level nor total exploration time predicted the total number of lids opened by the subjects (Table 1a). In addition, neophobia and explorative behaviour were not significantly correlated. However, age and the interaction factor age-neophobia level did show a significant effect on total lids opened (Table 1a). Consequently, the relationships between these behavioural variables and problem-solving ability were analysed separately for each age group. In juveniles, we found that neophobia level was the only significant predictor of the number of total lids opened (Table 1b and Fig. 7). Therefore, individuals that opened more lids also consumed food more quickly in the presence of a novel object. No significant relationship was observed neither between problem-solving ability and exploration behaviour (Table 1b) nor between these explanatory variables and the total number of lids opened in the case of adults (Table 1b).

Finally, the residuals of problem-solving performance (latency to open the first lid during D1) from neophobia level (latency to feed near a novel object minus the control latency) in juveniles were correlated with total exploration

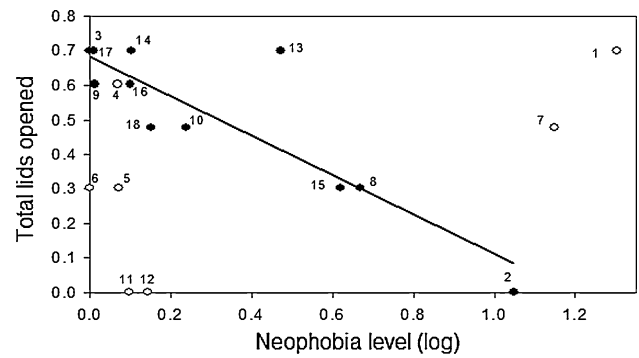


Fig. 7 Relationship between innovation ability, as measured by the total Plexiglas box lids opened, and level of object neophobia exhibited by juveniles of *M. chimango*. Black dots and regression line correspond to juveniles and white dots to adult individuals. Numbers identify each individual

time, to see if explorative behaviour is an intervening variable on the relation between problem-solving performance and neophobia level in this age group. This analysis did not demonstrate a significant relationship between residuals and exploration level (Pearson correlation, $n = 11$, $r = 0.14$, $P = 0.68$).

Discussion

In this study, we investigated three correlates of animal innovation: object exploration, neophobia level and novel problem-solving ability, in an opportunistic generalist raptor, the Chimango Caracara (*Milvago chimango*), taking

Table 1 Results from a general lineal model evaluating the relationship among problem-solving ability (response variable) and the continuous independent variables, level of neophobia (Neo) and explorative

Global model; $R^2 = 0.64$, $F_{6,11} = 3.309$, $P = 0.031$

	Neo	Exp	Age	Age \times Neo	Neo \times Exp	Neo \times Exp	Residuals
a							
df	1	1	1	1	1	1	11
Mean sq	0.016	0.012	1.642	1.977	0.022	0.0002	0.185
F value	0.084	0.066	8.883	10.699	0.119	0.001	
P	0.777	0.801	0.013	0.007	0.736	0.974	

Juveniles; $R^2 = 0.77$, $F_{2,8} = 13.67$, $P = 0.003$

	Neo	Exp	Residuals
b			
df	1	1	8
Mean sq	0.391	0.005	0.015
F value	27.02	0.33	
r	−0.52	−0.13	
P	0.001	0.582	

behaviour (Exp); (a) global model including age groups as categorical explanatory variable (b) separated models for adult and juvenile individuals

Adults; $R^2 = 0.39$, $F_{2,4} = 1.324$, $P = 0.362$

	Neo	Exp	Residuals
b			
df	1	1	4
Mean sq	0.17	0.009	0.068
F value	2.51	0.14	
r	0.32	−0.46	
P	0.188	0.727	

into account the inter-individual and age differences. Our findings show that behavioural responses in both, adult and juvenile birds, varied considerably among individuals. Juveniles showed a relatively higher propensity to explore natural and non-natural objects, and a lower neophobic response towards a novel object than adult birds. Individuals in both age groups were successful in solving the novel feeding problem, though we found shorter latencies to feed and a higher level of success in problem-solving tests in juvenile birds than in adult ones. Furthermore, individual performance improved after first solving the novel task, as indicated by the progressive reduction in feeding latency over the five session days and by the success in opening the lids during subsequent sessions. Finally, in juveniles, the problem-solving ability was inversely associated with object neophobia level; however, these variables were not related in adult birds. In both age groups, explorative tendency did not show a significant relationship with any of these behaviours.

Birds differed in their responses to the objects during the exploration test. Four of seven adult birds contacted only one object during the experimental session. In contrast, all juveniles explored between two and five different objects. Since adults and juveniles showed no statistical differences in their latencies to approach the objects, differences in exploration may not be attributed to the different neophobia levels shown by both age groups. Our results are in agreement with the patterns of behaviour described for the juvenile period, the stage when individuals show the greatest motor plasticity associated with object exploration and play (Greenberg 2003). This age period is also when such behaviours are more frequent and conspicuous (Greenberg and Mettke-Hofmann 2001; Greenberg 2003). In contrast, the minor exploratory activity in adults may have been more related to food recognition; while young birds may have contacted objects to investigate whether they were edible or not, adults may have already sufficient experience to determine that these objects were not a potential food resource (Negro et al. 1996).

Both juvenile and adult birds showed clear neophobic responses when confronted with a novel object close to the familiar food dish, as evidenced by the erection of neck feathers, postural changes and jumping jacks' behaviours. However, juveniles waited a shorter period before taking the meat from the dish, and their responses were less variable than those of adults. Neophobia is a widespread response in adult birds; however, its intensity varies considerably among closely related species (Laland and Reader 1999a; Greenberg 2003; Echeverria 2006; 2008) and among individuals within a species (e.g. Bouchard et al. 2007). Differences in neophobia level may result from complex environment–organism interactions during ontogeny (Greenberg 2003). The adults in this study showed a wide

range of novelty reactions, from non-response to a feeding latency comparable with the control situation values. We suggest that the variability observed among adult birds could be based on the different prior experiences of each individual, which, in turn, may have influenced the perceived cost and benefit of approaching the novel object. Furthermore, there is substantial evidence for a genetic background underlying the variation in neophobia, explorative behaviour and other aspects of animal temperament, such as aggressiveness and risk-taking behaviour (e.g. Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004; Fidler et al. 2007). Consequently, this may have been another factor contributing to the individual variability in responses to novelty observed in *M. chimango*.

The tendency to approach and explore novel objects is not enough to promote the development of new behaviours; these processes are necessary but not sufficient conditions for the emergence of an innovation. Individual learning (e.g. trial-and-error learning) follows the initial approach to the novel situation. The animal must then be able to associate the new behaviour with the particular novelty and to repeat the innovative performance, incorporating the new motor pattern and feeding preference into its foraging repertoire (Greenberg 2003). A previous study (Biondi et al. 2008) showed that young individuals of *M. chimango* have the capacity to obtain food in a novel situation. This ability was maintained and enhanced over subsequent sessions. Following an experimental methodology similar to the one used by Webster and Lefebvre (2001) for a Columbiformes and Passeriformes bird assemblage, Biondi et al. (2008) found that, when compared to the birds studied by Webster and Lefebvre (2001), juveniles of *M. chimango* took less time to approach and contact the Plexiglas box, responding faster and more successfully to a novel feeding problem. In the present study, we used the same experimental procedure as Biondi et al. (2008) but with the inclusion of adult individuals in the analysis. Our results show that both juvenile and adult *M. chimangos* were capable of solving the novel feeding problem and of enhancing their performance in time, although individuals in both age groups showed variable behavioural performances when solving a novel problem. These results are in agreement with Bouchard et al.'s study (2007) in pigeons.

In birds, it is well known that responses to novel objects correlate with feeding innovation, as measured by the amount of time needed to solve novel foraging tasks (Webster and Lefebvre 2001; Reader 2003; Lefebvre and Bolhuis 2003; Bouchard et al. 2007). In this study, problem-solving ability was negatively correlated with neophobia in young birds, but there was no relationship between these two behavioural attributes in adult individuals. This could be related to the fact that factors influencing innovative behaviour and object neophobia belong to different but

associated behavioural systems in juvenile birds, whereas in adult birds they do not. Alternatively, it should be noted that the sample size of adult subjects might have been too small to detect significant correlations.

The results of the exploration tests support several previous studies on the relationship between explorative behaviour and feeding neophobia (Greenberg 1984; Greenberg and Mettke-Hofmann 2001); we found that explorative tendency in *M. chimango* was not associated to object neophobia. Since exploration seems to be guided mainly by the potential value of the information to be attained, whereas neophobia seems to be more influenced by the cost of approaching the novel situation, these behavioural processes may yield non-correlated responses (Mettke-Hofmann et al. 2002, 2005a). In addition, though explorative behaviour has been considered to be related to innovation in animals, no clear correlation with problem-solving ability could be found. For example, though juveniles two and 15 were both highly explorative individuals, their latencies to first box opening fell among the maximum values registered for all individuals studied (Figs. 3 and 6). By contrast, individual 14 was one of the most explorative birds and also one of the fastest to solve the novel feeding problem. It is important to note that though the objects presented here do not represent a common feeding resource to these birds, some individuals might have had experience with some of these objects in the wild. Experiments with more novel objects, or experiments involving active spatial exploration that would require information-gathering, might more accurately reveal the relationship between exploration and problem-solving. For example, Boogert et al. (2006) found that, in a captive group of wild-caught starlings (*Sturnus vulgaris*), individual learning performance in a feeding task correlated with the latency to feed in a novel environment, but not with the latencies to feed near a variety of novel objects. Moreover, even though both types of neophobia were measured in the same foraging context, they were not significantly correlated with each other.

In conclusion, this is one of the few studies exploring age and inter-individual differences in behavioural innovation and their correlates in a bird of prey, *M. chimango*. Juvenile and adult birds showed a highly variable propensity to explore a series of objects without an immediate food reward. Young birds exhibited both a marked exploratory behaviour and a relatively low neophobic response towards the presence of a novel object close to the familiar food source. Moreover, both adults and juveniles coped with a novel feeding problem with high success, although young birds were on average more proficient than adults. Since juvenile *M. chimango*, like other birds of prey (Newton 1979), must disperse from their natal area to novel territories after fledging, high curiosity, low neophobia, and

the ability to innovate could have potentially significant benefits. Gregariousness in these species, particularly those relating to foraging (Fraga and Salvador 1986; White et al. 1994; Ferguson-Lees and Christie 2001), enhances the likelihood that an acquired behaviour could be transmitted among population members. Such acquisition and transmission of novel behaviours may be one of the factors underlying the ecological success shown by this opportunistic and generalist Neotropical raptor.

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