The Effect of Age and Sex on Object Exploration and Manipulative Behavior in a Neotropical Raptor, the Chimango Caracara, *Milvago chimango*

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Abstract

We studied object exploration and manipulative behavior in wild-caught Chimango Caracaras (*Milvago chimango)*, an opportunistic and generalist raptor species, in relation to age and sex differences. Each bird was presented with six objects. We then recorded the latencies to approach and first contact with the objects, the number of objects explored, and the number of exploration events performed on each object. Age influenced the tendency to explore in *M. chimango*. Compared with adults, juveniles were more likely to explore the objects, approaching and contacting them more quickly. The number of objects explored was also higher in young than adult birds. Both age classes used a variety of manipulative behaviors to explore the objects, some of which have been described as play in others studies. Sex did not affect an individual's likelihood to explore or the number and frequency of manipulative behaviors used during object exploration. The tendency for both young and adult birds to explore and manipulate objects that not resemble prey is likely to be a distinct advantage for a generalist species like *M. chimango* which must cope with a high diversity of modified environments.

Introduction

The ability to adapt to unfamiliar and novel situations is a primary requirement for animals living in complex and changing environments, in which uncertainty is an unavoidable characteristic (Inglis 2000; Inglis et al. 2001). Explorative behavior is a way to learn about the features of the environment and thus decrease uncertainty (Hughes 1997; Greenberg & Mettke-Hofmann 2001; Yosef & Pinshow 2005). Consequently, exploration may have a significant effect on future decision-making events (Barnett 1963).

It is generally accepted that familiarization with the environment through exploration provides information about resources for future reference (Barnett 1963) possibly by enabling the establishment of cognitive models to assist in later searching behavior (Bell 1991). Novelty is one of the most important characteristics of a stimulus that is capable of evoking and maintaining an explorative response (Berlyne 1950; Hughes 1997). In natural situations, many of the decisions that animals make involve resources that are qualitatively novel and to varying degrees dissimilar from what they have previously experienced. These include the appearance of a new prey type which has a bold and unusual color pattern; the seasonal progression of fruits, flowers, and vegetative structures; new habitats encountered during seasonal migration and dispersal; and environments produced by rapid anthropogenic changes. Novelty is a unique transitory quality based on the experience of the individual and not on the intrinsic value or danger of the novel stimulus itself. The benefit of exploration depends on the value of the information to be extracted, which is closely related to current resource requirements, as well as the level of environmental uncertainty and risk perceived (Greenberg &

Mettke-Hofmann 2001; Danchin et al. 2004). Consequently, factors, such as age, sex, type of habitat occupied, and reproductive state, may potentially influence the assessment of a novel situation before an individual makes a decision and acts accordingly.

There are many definitions of explorative behavior in the literature (Hughes 1997). An important distinction made by Berlyne (1960) was between extrinsic and intrinsic exploration. Extrinsic exploration was defined as a behavior that is primarily directed toward an external goal in response to some specific requirement. It involves active seeking of a particular outcome such as finding food when hungry or handling prey. On the other hand, intrinsic exploration is considered as a behavior that facilitates investigation of stimuli mainly in response to an interest in these stimuli for their own sake. It comprises *inspective exploration*, in which the animal responds to an environmental change, and *inquisitive exploration*, in which the animal acts in order to make a change (Russell 1983), is looking for something (Berlyne 1960), or perfecting a behavioral adaptation (Yosef & Pinshow 2005).

One of the best ways of studying animals' intrinsic exploration is through observations of their investigation of novel objects, usually within a less novel or familiar home environment. (Hughes 1997). A wealth of information about the precise details of exploratory responses in animals can be obtained by carefully recording the nature of their interactions with objects. This information may aid in the development of learning models and can lead to a better understanding of the biology of these processes (Renner 1990). In addition, the actions performed by an individual during active object manipulation enable the development of object recognition and memory (Pereira et al. 2008).

The inclusion of aspects of the interaction with objects in explorative behavior studies may increase the complexity of the analysis. Yet, an effort to incorporate more detail in the observations is necessary if we are to achieve a functionally valid description of exploration. This involves the quantification of not only spatial exploration, but also other forms of object investigation and manipulation (Renner 1990; Hughes 1997). For an exploring individual, a complete memory for objects in the environment would also include knowledge about their physical characteristics and what expectancies are associated with them. This, in turn, requires an active investigation of inanimate features of the environment as well as their locations. Any view of exploration that sees it as related to learning must recognize that the particular behaviors of the exploring organism, or behavioral

topography, can play a critical role in the nature and quantity of information obtained (Renner 1990).

The Chimango Caracara, *Milvago chimango*, is a Neotropical falconiform whose ecological plasticity is well known (Ferguson-Lees & Christie 2001; Biondi et al. 2005). However, information about its cognitive abilities has been assessed through experimental studies only recently (Biondi et al. 2008, 2010a,b). This raptor is a gregarious species which inhabits a broad geographical range and a wide diversity of habitats. It may therefore be expected to show considerable behavioral flexibility, perhaps partially acquired through exploration and play during early life stages (Ortega & Bekoff 1987). Indeed, previous experimental studies in aviaries have shown that there is a marked difference between adults and juveniles of *M. chimango* in their tendency to explore when confronted with novel objects. However, this analysis considered only latency values, thus providing an incomplete description of exploratory behavior. Here, we analyze the effect of age and sex on explorative behavior of novel objects in wild-caught individuals of *M. chimango*. We focused on the behavioral topography of object manipulation performed by each individual, and its relationship with the information-gathering process and functionality.

The benefits of approaching and exploring novel situations appear to differ for juveniles and adults (Biondi et al. 2010a), possibly due to differences in past experiences in similar situations. As a result, these two age groups are likely to show differences in their exploratory behavior. Similarly, as males and females of *M. chimango* play different roles in reproduction, and consequently different incentives to explore their environment, we predicted that males and females differ in their willingness to take risks and to explore new stimuli. The amount and quality of information gathered throughout exploration depends on the form of manipulative behavior during exploration (Power 2000; Kootstra et al. 2008). Therefore, if the propensity to explore new stimuli differs between sex and age classes, it is also likely that these groups differ in the amount of information extracted by their distinctive topographies of explorative behavior performed on the objects.

Methods

Nineteen adult birds (>2 yrs old; nine females and ten males) and seventeen juveniles (<1 yr old; 11 females and 6 males) were caught with baited walk-in traps (Bloom 1987) in a suburban area, 20 km from the closest city (Mar del Plata, Argentina) between March

and August (non-breeding period) of 2008–2010. Plumage color (mainly of rectrices), tarsus color, and molt stage were used to determine age (White et al. 1994; Ferguson-Lees & Christie 2001). Housing and care conditions followed Bloom (1987) and Aprile & Bertonatti (1996). Birds were identified with leg bands, weighed, and a blood sample was taken from the brachial vein to perform molecular sexing (Fridolfsson & Ellegren 1999). Each bird was then housed in an individual outdoor aviary (2 × 1.5 × 1.5 m). The aviaries were visually isolated from one another by a synthetic black fabric, ensuring that the individuals acted without social motivation. To become habituated the birds to captivity, they were given a period during which they were fed once a day from a dish containing beef and chicken meat, and water was provided *ad libitum*. The individuals were considered to be habituated when they were comfortable enough to feed shortly after presentation of the food (Biondi et al. 2008, 2010a,b). This period was less than 1 wk in all cases. All individuals were released at the capture sites at the end of the experiments.

Experimental Procedure

One hour before the trial, all birds were fed with the same amount of meat (60 g), which is the quantity needed to satiate a captive bird of the size of *M. chimango* (Biondi et al. 2008). It is important to clarify that it is often difficult to experimentally distinguish between extrinsic and intrinsic exploration because the responses emitted can be identical (Hughes 1997). However, working with satiated birds increases the chance of observing exploration that occurs for its own sake, and not by the necessity to find food or water (Wood-Gush & Vestergaard 1991; Hughes 1997). To accomplish this, we ensured that the birds had eaten all the food given before starting the trial, so no food was present inside the aviaries during the experiments.

The birds were given six objects: a dry starfish, a dry limpet shell, a walnut, a red cigarette box (closed and empty), a yellow plastic container (8 × 5 cm, open and empty), and a black plastic bag closed and filled with a load (10 × 7 cm). The objects were randomly distributed on the aviary floor and separated by at least 20 cm. Each bird was given 15 min to explore the objects during a single experimental session. We recorded the following variables: (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 contact with an object (with either the bill or feet); (3) total number of objects contacted; and (4) total exploration time for each individual. Explorative behavior was considered to have ceased when the individual walked away without paying further attention to the objects or 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 also considered as an explorative event situations in which an individual approached the objects and visually inspected them, without making contact. In this case, the exploration was considered to be finished when the individual paid no further attention to the objects, moving away to another location in the aviary or perching. To analyze the topography of the explorative behavior, the exploration period recorded for each individual was divided into discrete explorative events. Each event consisted of the action of contacting one object in a persistent manner. When the subject stopped making contact with the object for at least 10 s or moved to another object to handle it, the event was regarded as finished.

Manipulative behaviors performed during object exploration were grouped into categories according to the discrete actions performed by the birds: (1) Visual exploring with simple contact with the talons or bill; (2) grabbing an object with the talons and pecking it; (3) transporting the object; and (4) throwing the object to the floor and retrieving it immediately after. A more detailed description of these behaviors is provided in Results. The frequency of these exploration categories was assessed and analyzed for each explorative event performed by the individuals.

General Statistical Analysis

We assessed the effect of age and sex on latency values and total exploration time using generalized linear models (GLM). These models were constructed with the interaction between age class (adults, juveniles) and sex as explanatory variables, and the behavioral responses (approach and contact latencies, exploration time, number of objects explored and number of exploration events) as response variables. Latency time and total exploration time were converted to proportions, by dividing by the total experiment time (900 s). As we worked with proportions, a binomial error structure and logit link function was used for time-related response variables (Crawley

2007). In models that included the number of objects contacted and the quantity of exploration events as response variables, we used a poisson error structure with a log link function, because it is the most appropriate error structure family and link function for a count variable (Crawley 2007). We also used GLM to compare the diversity of manipulative behavior categories, between age and sex classes. In this case, the number of different categories used by each individual was included as a response variable. A poisson error structure and log link function was selected for this analysis. In addition, generalized lineal mixed models (GLMM) were performed to evaluate the variation in the relative frequency of use of each behavioral category showed by adult and juvenile birds. To calculate this value, we divided the times that one particular category was used by an individual with the total of times that a category was chosen during all exploration events recorded for that bird. We included individual identity as a random factor and category and age classes as explanatory variables. A binomial error structure and logit link function was used for this response variable (Pinheiro & Bates 2000; Crawley 2007). Model fitting was visually assessed by inspecting plots of standardized deviance residuals for each model. We assessed goodness of fit for all models and estimated the variance inflation factor (ĉ) as residual deviance divided by degrees of freedom (Burnham & Anderson 1998). All analyses were carried out using R, Version 2.15.0 (R Development Core Team 2008). Values were presented as mean ± standard error.

Results

Young birds were more exploratory than adult birds, although adults showed a notable interindividual variability in their responses. Whereas all juveniles approached the objects and touched at least one of them during the experiments, only 42% of adult birds showed explorative behavior (Binomial test; approach: $\chi^2 = 4.37$, df = 1, p = 0.037; contact: $\chi^2 = 11.57$, df = 1, p < 0.001). Of 11 adults that did not explore any objects, six stayed on their perches

during the experimental session; the other five adults approached the objects but returned to their perches immediately after examining the objects for a few seconds. There were no differences between males and females in the proportion of individuals that approached (87% males vs. 80% females; Binomial test: $\chi^2 = 0.02$, df = 1, p = 0.881) and contacted (69% males vs. 70% females; Binomial test: $\chi^2 = 0.15$, df = 1, p = 0.698) at least one object.

Mean latency to approach the objects was 20 ± 2 s. Adults (20 ± 2 s) and juveniles (21 ± 3 s) did not differed in latency to approach (Table 1), nor did males (20 ± 3 s) and females (20 ± 2 s; Table 1). Mean latency to contact the objects was 14 ± 2 s. Comparisons in contact latency between adult (16 ± 3 s) and young birds (13 ± 3 s) and between males (15 ± 3 s) and females (12 ± 3 s) did not yield significant differences (Table 1). There was no effect of the interaction between sex and age factors (Table 1).

Exploration time ranged from 10 to 532 s, with a mean value of 120 ± 20 s. There was a significant difference between adults and juveniles (Table 1): youths explored the objects for longer times than did adults (Fig. 1a). Males (134 ± 44 s) and females (108 ± 22 s) did not differ significantly in the total exploration time, and there was no significant interaction between age and sex (Table 1).

There was a high interindividual variability in the total number of objects contacted, which ranged from 1 (four individuals) to 6 (two individuals) (x̄ = 2). Adults explored fewer objects than did juvenile birds (Fig. 1b, Table 1). Male (3 ± 0.6) and female (3 ± 0.4) birds did not differ in this variable (Table 1). Once again, there was no interaction between age and sex (Table 1).

The average number of exploration events performed by the birds was 7.68 ± 1.12. Young birds performed significantly more events than did adults (Fig. 1b, Table 1). Sexes did not differ in this variable (males: 8.18 ± 2.32 vs. females: 7.29 ± 1.37; Table 1), and there was no interaction between age and sex (Table 1). Additionally, some of the objects

Table 1: Generalized linear models results from the comparison between age and sex, as well as their interaction of behavioral variables registered during exploration tests. Individuals that not explored any object were excluded from the models

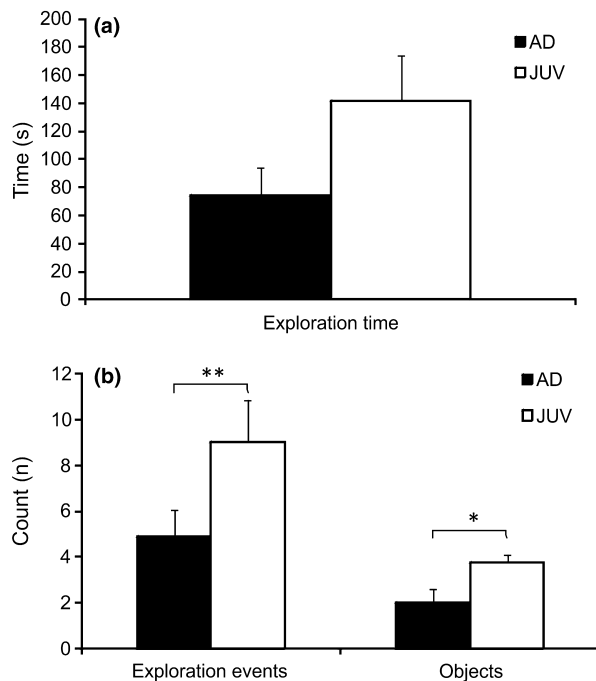|	Approach		Contact		Time		N obj		Events	
	t	p	t	p	t	p	z	p	z	p
Age	−0.7	0.474	0.3	0.797	2.3	0.030	2.5	0.011	2.8	0.006
Sex	−1.2	0.264	0.8	0.462	1.3	0.211	1.2	0.217	1.1	0.313
Age:Sex	1.5	0.156	−0.6	0.584	−0.5	0.661	−0.4	0.665	−0.1	0.889

Fig. 1: Comparison between adults and juveniles in (a) total exploration time (means ± SE) and (b) quantity of exploration events and objects contacted during the experimental test. A single asterisk means statistically significant differences of p < 0.05, two asterisks represent a probability value lower than 0.01.

elicited more exploration events than others (Table 2). Adults showed a clear tendency to explore the plastic container more frequently (Fig. 2), while juveniles performed significantly more exploration events on the dry limpet shell (Fig. 2). The proportion of events devoted to the rest of the objects was similar for both ages (Table 2).

Four distinct topographies, or manipulative behavior categories, were observed during the exploration events performed by the birds. All categories were preceded by the bird's approach to a particular object (usually leaving its perch), as well as by close visual inspection (less than 5 cm). (C1) Then, the animal typically contacted the object with the bill or talons, slowly or by continuous pecks and scratches. (C2) After this first contact, the majority of birds used one or both legs to approach and firmly hold the object close to the body, continuing to peck it. Birds usually rotated the object with the bill, always holding it with the talons and continuing to peck at different parts of the object. (C3) In several other cases, the bird took an object with the bill and transported it to another location in the aviary. This was not always preceded by the occurrence of behavioral categories 1 or 2. After placing the object on the floor, the individual

grasped it with the talons and started pecking or scratching it. This behavioral pattern was followed in several occasions by the same sequence of actions as before, but preceded by the transportation of the object back to their original location. (C4) Another form of manipulation was represented by an individual lifting an object with his beak and throwing it vigorously on the floor at approximately the same place. This action was repeated many times during the same exploration event.

The first category (C1) was used at least in one occasion by all juveniles and by 87% of adult individuals that explored the objects. The second category of manipulative behavior (C2) was recorded in 70% of juveniles and in 50% of adult birds. C3 was used by 65% of young individuals and by 35% of adults, whereas the fourth category was seen in 70% of juveniles and in 75% of adult birds. Juveniles also showed a higher diversity of behaviors than adults during the experimental test. They used an average of 4 ± 0.3 of the four categories registered, whereas adults used 2 ± 0.4 of these categories to manipulate the objects presented (GLM, $z = 3.4$; $p < 0.001$). There was no difference in these variables between males (2 ± 0.5) and females (2 ± 0.4) (GLM, $z = 1.5$; $p = 0.148$), and the interaction between these factors was not significant (GLM, $z = -1.1$; $p = 0.294$).

Compared with the rest of the behavioral categories recorded, C1 was used more frequently (Table 3), that is, the animal contacted the object with the bill or talons, slowly, or by continuous pecks and scratches. The second more frequent behavioral category was C2 (the bird walked to the object and held it close to the body, continuing to peck it), but these values were not statistically different from the other categories (Table 3). This general pattern persisted when this analysis was performed including age as a factor. However, the GLMM revealed that the difference between the C1 and the rest of the categories was observed only in juveniles, while in adults, these differences were only slightly significant (Table 3). Taking into account the frequency values of each category (Fig. 3) and the fact that the p values for these comparisons approached statistical significance, the lack of significant differences in adults between C1 and the other categories was probably due to the low number of individuals in this age group that contacted the objects.

The frequency of each behavior category also varied with the particular object explored. In general, the higher values were observed during the manipulation of the limpet, the plastic container, and the dry starfish, compared with the rest of the objects

Table 2: Fixed-factor contrasts resulted from GLMM comparing objects in term of frequency of use of the behavioral categories (C1–C4), as well as quantity of exploration events performed by adults and juveniles. In each model, individual identity was included as a random factor

Contrasts between categories	C1		C2		C3		C4		Events	
	z	p	z	p	z	p	z	p	z	p
Adults										
Bag − Container	−3.7	<0.001	−1.2	0.212	0.9	0.378	−1.4	0.152	−2.1	0.033
Box − Container	−3.9	<0.001	−2.8	0.042	NA	NA	NA	NA	−2.2	0.028
Starfish − Container	−1.5	0.135	−2.2	0.031	0.5	0.600	0.3	0.769	−2.2	0.028
Limpet − Container	−2.5	0.010	−1.5	0.127	NA	NA	−0.7	0.495	−2.1	0.038
Walnut − Container	−3.9	<0.001	NA	NA	NA	NA	−1.1	0.285	−2.1	0.032
Bag − Box	1	0.328	0.7	0.491	NA	NA	NA	NA	0.5	0.598
Starfish − Box	3.1	0.002	−0.9	0.349	NA	NA	NA	NA	−0.1	0.973
Limpet − Box	2.4	0.016	0.4	0.711	NA	NA	NA	NA	0.6	0.538
Walnut − Box	0.4	0.707	NA	NA	NA	NA	NA	NA	−0.1	0.896
Bag − Limpet	−2.4	0.031	0.3	0.743	NA	NA	−0.9	0.353	0.6	0.578
Starfish − Limpet	1.2	0.241	−1.2	0.222	NA	NA	0.9	0.339	0.6	0.520
Walnut − Limpet	−2.2	0.028	NA	NA	NA	NA	−0.4	0.665	−0.1	0.923
Bag − Starfish	−2.7	0.007	1.4	0.148	0.4	0.680	−1.6	0.106	−0.1	0.920
Walnut − Starfish	−3.0	0.002	NA	NA	NA	NA	−1.3	0.189	−0.7	0.475
Bag − Walnut	0.6	0.531	NA	NA	NA	NA	−0.5	0.581	0.6	0.527
Juveniles										
Bag − Container	−2.6	0.009	−0.9	0.323	0.3	0.787	0.0	1.000	−0.1	0.911
Box − Container	−1.9	0.046	−1.2	0.228	−0.6	0.540	−0.3	0.744	−0.6	0.531
Starfish − Container	−0.9	0.342	−0.8	0.437	−0.9	0.339	1.4	0.151	1.9	0.049
Limpet − Container	2.9	0.003	4.8	<0.001	2.1	0.033	3.3	0.001	−0.3	0.791
Walnut − Container	−3.1	0.002	−2.1	0.034	NA	NA	NA	NA	−0.9	0.322
Bag − Box	−0.7	0.509	0.2	0.819	0.9	0.384	0.3	0.744	0.5	0.602
Starfish − Box	1.1	0.288	0.4	0.657	−0.4	0.713	1.7	0.088	2.3	0.020
Limpet − Box	4.7	<0.001	5.3	<0.001	2.5	0.011	3.4	0.001	0.4	0.710
Walnut − Box	−1.2	0.219	−1.1	0.294	NA	NA	NA	NA	−0.4	0.664
Bag − Limpet	−5.2	<0.001	−5.3	<0.001	−2.1	0.044	−3.3	0.001	−2.1	0.041
Starfish − Limpet	−3.8	<0.001	−5.2	<0.001	−2.7	0.007	−2.3	0.019	−2.1	0.032
Walnut − Limpet	−5.6	<0.001	−5.3	<0.001	NA	NA	NA	NA	−2.4	0.018
Bag − Starfish	−1.9	0.048	−0.2	0.828	1.2	0.231	−1.4	0.151	0.2	0.877
Walnut − Starfish	−2.2	0.025	−1.5	0.146	NA	NA	NA	NA	−0.8	0.440
Bag − Walnut	0.6	0.565	1.3	0.208	NA	NA	NA	NA	−0.9	0.368

(Table 2). This analysis was also performed in adults and juveniles separately, to assess if the general pattern found for all individuals was also similar for both age classes (Table 2). Although the major frequency of each behavioral category was observed for the limpet and the plastic container, the relative values of each category used on these two principal objects did not exactly match between adult and juvenile birds (Fig. 4). For example, adults more frequently used with the first and second categories to manipulate the container; the 'transportation of the object' (C3) was only used in the plastic bag, container, and dry starfish; and the category 'lifting and throwing the object' (C4) was used in a similar proportion with all the objects, excluding the box. Juveniles interacted with the limpet shell most frequently for all categories of manipulation (Fig. 4). The rest of them were observed

with similar values in all objects, with the exception of the walnut for which C3 and C4 were never used. These results also indicated that particularly in these objects—the limpet and the container—the individuals showed the highest diversity of behavioral topographies.

Discussion

In this study, we analyzed object exploration and manipulative behavior topographies in relation to age and sex for an opportunistic generalist raptor, the Chimango Caracara (*Milvago chimango*). This analysis was performed in satiated individuals, so intrinsic exploration could be measured. Our findings showed that age influenced the tendency to explore in *M. chimango* and that this response was highly dissimilar
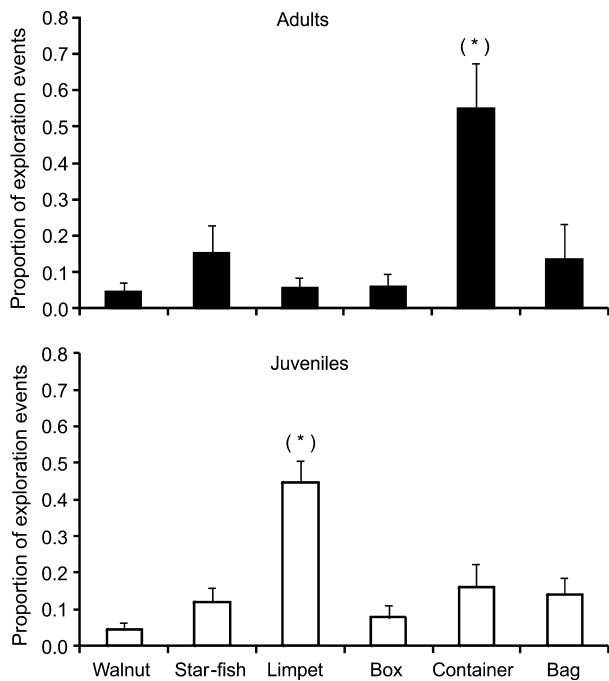
Fig. 2: Proportion of exploration events performed on each object by adults and juveniles. The asterisk means differences of $p < 0.05$ between that object and the rest of them.

Table 3: Fixed-factor contrasts resulted from GLMM comparing the relative frequency of use of the behavioral categories (C1–C4) in all individuals, as well as in adults and juveniles separately. In each model, individual identity was included as a random factor

Contrasts between categories	General		Adults		Juveniles	
	z	p	z	p	Z	p
C1–C2	−3.1	0.002	−1.8	0.064	−2.4	0.015
C1–C3	−3.5	0.001	−1.9	0.057	−2.9	0.004
C1–C4	−3.3	0.001	−1.6	0.107	−2.9	0.004
C2–C3	−1.1	0.255	−0.6	0.546	−0.9	0.333
C2–C4	−0.5	0.638	0.4	0.706	−0.8	0.399
C3–C4	0.7	0.474	0.9	0.372	0.2	0.884

Fig. 3: Comparison between behavioral categories (C1–C4) in the relative frequency values (means ± SE) showed by adults and juvenile birds of *M. chimango*. Different letters indicate statistically significant differences ($p < 0.05$).

Fig. 4: Comparison of the frequency of use of each behavioral category between objects performed by adult and juvenile birds. Different letters represent statistically significant differences ($p < 0.05$) in the frequency of a category between objects.

across individuals. In this context, birds differed in their initial responses to the objects during the exploration test. While all juveniles explored at least one object during the experimental test, only half of the adult birds approached and contacted the objects. Both young and adults birds used a variety of behavior categories to explore the objects; however, juveniles exhibited a higher diversity of manipulative behaviors. We did not observe a significant effect of sex on the decision to explore or in the number and
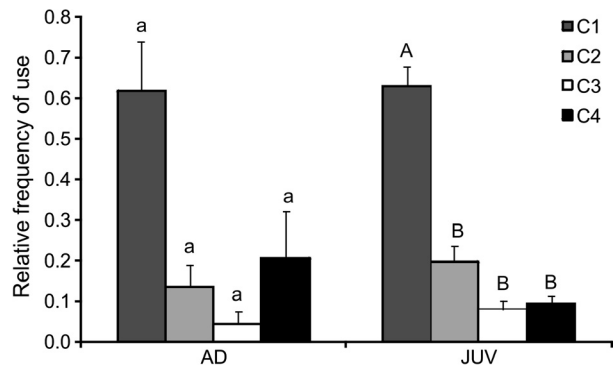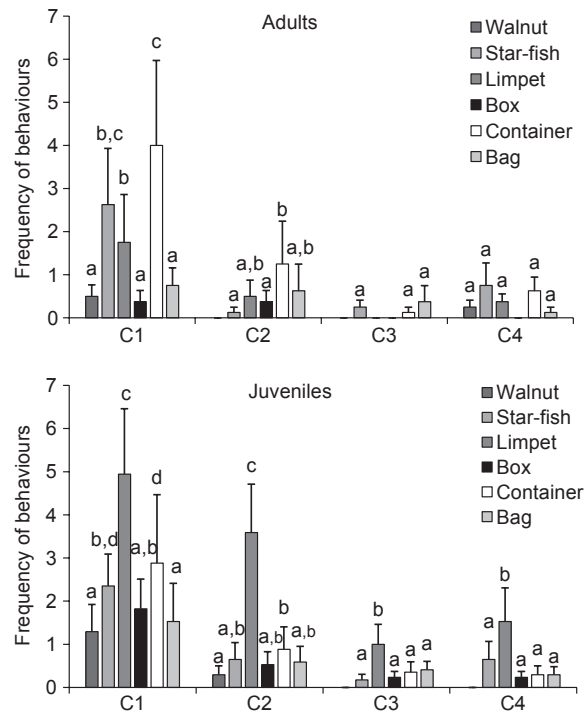
frequency of manipulative behaviors used during object exploration.

Exploration is a part of an animal's information processing that is usually defined as a behavior that reduces uncertainty about the external environment through information gathering (Cowan 1976; Weisler & McCall 1976; Renner 1990). It typically occurs

upon an animal's initial exposure to an object or environment, or when some changes in the surroundings have occurred (Berlyne 1950). Exploration, however, is not the only common response to novelty; fear and avoidance (neophobia) can also result (Barnett 1958; Menzel 1965). The degree of neophobia varies with the ecological plasticity of the species and the type of habitats in which they occur (Greenberg 1990; Mettke-Hofmann et al. 2002). Generalist species, such as *M. chimango*, benefit from being less neophobic and more explorative compared with ecological specialists, because they are able to take advantage of novel resources and feeding opportunities (Greenberg 1983, 2003; Mettke-Hofmann et al. 2002). Indeed, a previous study of *M. chimango* response to novelty found that most individuals were immediately curious about the objects presented, contacting at least one of them during the experiment (Biondi et al. 2010a). However, the initial response to the objects was highly variable across the individuals that were tested here. This variability seemed to be linked to the difference between age groups. The number of individuals that showed explorative behavior was markedly higher in juveniles than in adult birds. These results might indicate that the observed variation in the decision to explore can be attributed in part to differences in neophobia between age classes.

A number of studies of both avian and non-avian species have demonstrated that individuals show consistent and often dramatic differences in fearfulness (Meaney 2001; Fox & Millam 2007). Adult birds studied here showed a wide range of novelty reactions, from non-response to short approach and contact latencies similar to those of the most curious juveniles. We suggest that this variability within adults may be related to the different prior experiences, which, in turn, may have influenced the perceived cost and benefit of approaching objects. Another source of variability in the tendency to explore may result from intrinsic individual differences in behavioral type or 'personality' (Verbeek et al. 1994; Wilson 1998). There is substantial evidence for a genetic background underlying the variation in neophobia, explorative behavior, and other aspects of animal personalities (Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004; Fidler et al. 2007). Is important to note, however, that there is growing evidence that personality is less temporally stable than was often assumed and can be modified by prior experiential factors at different ages or life stages of an individual (Stamps & Groothuis 2010; Groothuis & Trillmich 2011). Young and adults may live in different ecological niches and therefore may have different selection

pressures. Consequently, it is to be expected that if the organization of behavior in personalities is beneficial for survival, young animals may have different ones than adult animals (Stamps & Groothuis 2010; Groothuis & Trillmich 2011). In this sense, the high variability in explorative behavior found in individuals of *M. chimango* may have resulted from complex environment–organism interactions during ontogeny (Greenberg 2003; Groothuis & Trillmich 2011), which also may explain the difference between ages in the tendency to explore and why adults showed more diverse responses to novelty compared with young birds.

Age differences in exploration were also showed in the other behavioral variables recorded; juveniles expended more time exploring a larger number of objects and performed a higher number of exploration events than adults. These results could be interpreted as a more persistent and thoughtful investigation of the environment's elements in juveniles. It might be suggested that in this way juveniles extracted a greater amount of information from the objects than adults did; or at least they needed a greater number of exploration events to get an estimation of its value. Alternatively, it may be that after the juveniles first inspect an object, subsequent encounters with the same object may be related to instances of play. In fact, play behavior has been considered as a form of manipulation which is generally preceded by exploration (Power 2000). During exploration and play, new behavior sequences can emerge, which serve as the raw materials for developing innovative forms of problem-solving and tool use (Fagen 1981; Ortega & Bekoff 1987; Power 2000). This might result in the enhancement of cognitive and behavioral flexibility development particularly in young individuals of *M. chimango,* which performed these behaviors more frequently. Indeed, the juvenile stage is when individuals show the greatest motor plasticity associated with object exploration and play and when such behaviors are more frequent and conspicuous (Greenberg & Mettke-Hofmann 2001; Greenberg 2003). In contrast, the more superficial exploratory behavior recorded in adults may have been more related to experience and stimuli recognition; adults may have already sufficient experience to categorize and determine that these objects were not a potential food resource (Negro et al. 1996; Biondi et al. 2010a).

It was previously hypothesized that sex could be another factor that influences the explorative tendency and behavior showed by individuals of *M. chimango*. For example, in primates sex has been shown to influence responsiveness to environmental stimuli

and to correlate with levels of interest in novel objects (Fragaszy & Visalberghi 1990). In birds, Range et al. (2006) have found that male ravens showed a higher number of manipulative actions and shorter approach latencies when confronted with an object baited with food inside. These sex-related differences in response to novelty have been related to sex-specific physiological demands and to differential investment during the reproductive period (Greenberg & Mettke-Hofmann 2001; Stöwe et al. 2006). In this study, the decision to explore and the initial reaction to the objects presented was not affected by the sex of individuals. In *M. chimango,* there is no a clear dominance mediated by size or sex (females are only slightly bigger than males), and there are no gender differences in parental investment during the breeding period (Fraga & Salvador 1986; Morrison & Phillips 2000). Therefore, these could account for similarities between sexes in risk-taking decisions and, consequently, in explorative behavior.

All forms of manipulation observed in this work might be interpreted as inquisitive exploration, because all of them began with the animal's first approaching and visually inspecting the objects (Hughes 1997). The first two behavioral categories, contacting and holding the objects (C1 and C2), are actions which could serve to gather information needed for the objects' recognition. Hence, it should be no surprise that these categories were the most frequently used by individuals of *M. chimango*. These behaviors have been documented elsewhere as the most common types of manipulations performed during object play in raptors (Negro et al. 1996; Kitowski 2005). The transporting and throwing the object (C3 and C4) are indicative of more active physical contact with the objects. It seems that these actions may have provided further information about the object and its components, for example, that additional features could be revealed as a result of breaking the object. The transportation of objects was observed in other bird species and categorized as play behavior. This is the case of adult and juvenile individuals of Neotropical Cormorants, which were observed walking a few steps while holding a branch in its bill and then releasing the branch to pick it up again (Sazima 2008). Here, the transportation of an object occurred always from the center of the aviary, where all objects were presented, to one of their extremes and then come back to the original location. Individuals separated the object from the rest before they started pecking it, then they returned it to the group and continued pecking it. To our knowledge, this spatial and temporal pattern of object exploration was not previously described for birds or mammals. Consequently, although further studies should be carried out to analyze this topic in more detail, it seems possible that the function of these actions might be related to the process of recognition and identification of the object, particularly through its individualization and its posterior comparison with the other elements of the aviary (active grouping).

Several attributes of the stimulus itself are considered crucial to elicit explorative behavior (Power 2000; Mettke-Hofmann et al. 2006). Physical properties of the stimulus, like size and complexity, have also been observed to influence the decision to investigate an object (Berlyne 1950; Weisler & McCall 1976). In this study, individuals were more likely to explore the dry limpet shell and the plastic container than any of the other objects presented. These objects are both conical in shape and have an opening on the base which can be inspected by introducing the bill or feet. None of the other objects had a shape with conspicuous volume and concavities. Therefore, it may be that the preference showed by the individuals for these two objects was due to the opportunity of exploring not only its surface, but also its content. Moreover, these objects could be easier for the individuals to grip and handle, compared with the other objects. This was also supported by the fact that both preferred objects were those for which individuals showed the highest diversity of manipulative topographies.

Object manipulation has been widely observed in juveniles of many species of raptors, although rarely recorded in adults (Bildstein 1980). For this group of predators, object manipulation and play has been hypothesized to be a mechanism by which young animals acquire and develop prey hunting and handling skills (Fagen 1981; Bekoff & Byers 1992). These behaviors are particularly common among agile and maneuverable raptors (Simmons 1984; Johnson 1986; Komen & Meyer 1989; Bustamante 1993, 1994, 1995; Kitowski 2005). By contrast, object manipulation has rarely been observed in raptors whose habitual food is widely available (e.g., insects) and easy to obtain (e.g., carrion) (Donazar & Ceballos 1990; Bustamante & Negro 1994; Koga & Shiraishi 1994). *M. chimango* is a opportunistic raptor that preys mainly on insects, but also consumes other arthropods and small vertebrates, as well as feeding on carrion and human refuse (Cabezas & Schlatter 1987; Biondi et al. 2005). Due to its diet and the morphology of its trophic apparatus, it is not considered a predatory bird with highly specialized hunting techniques (Ferguson-Lees & Christie 2001; Biondi 2010). However, in

this work not only juveniles but also adult individuals of *M. chimango* were observed manipulating objects, using a diversity of behavior topographies, some of them complex and resembling those classified as play in other studies (Negro et al. 1996; Sazima 2008). As far as we know, this is the first study evidencing exploration and manipulation of objects that are unlike prey in both juveniles and adults in a bird of prey. These kinds of actions, performed by birds that can be confidently assumed to be satiated, reflect the highly curious nature of this raptor. Moreover, this kind of behavior may be related to the expectance of a high increase in information through exploration, which is a common characteristic of complex and heterogeneous habitats (Mettke-Hofmann et al. 2002). High curiosity and explorative tendency, the ability to perform behavioral innovation, and the individual and social learning capacities observed in previous studies (Biondi et al. 2008, 2010a,b), are all probably of great advantage for a generalist species like *M. chimango*, who have to cope with a high diversity of modified or novel environments such as urban areas (Ferguson-Lees & Christie 2001; Biondi et al. 2005).

Acknowledgements

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