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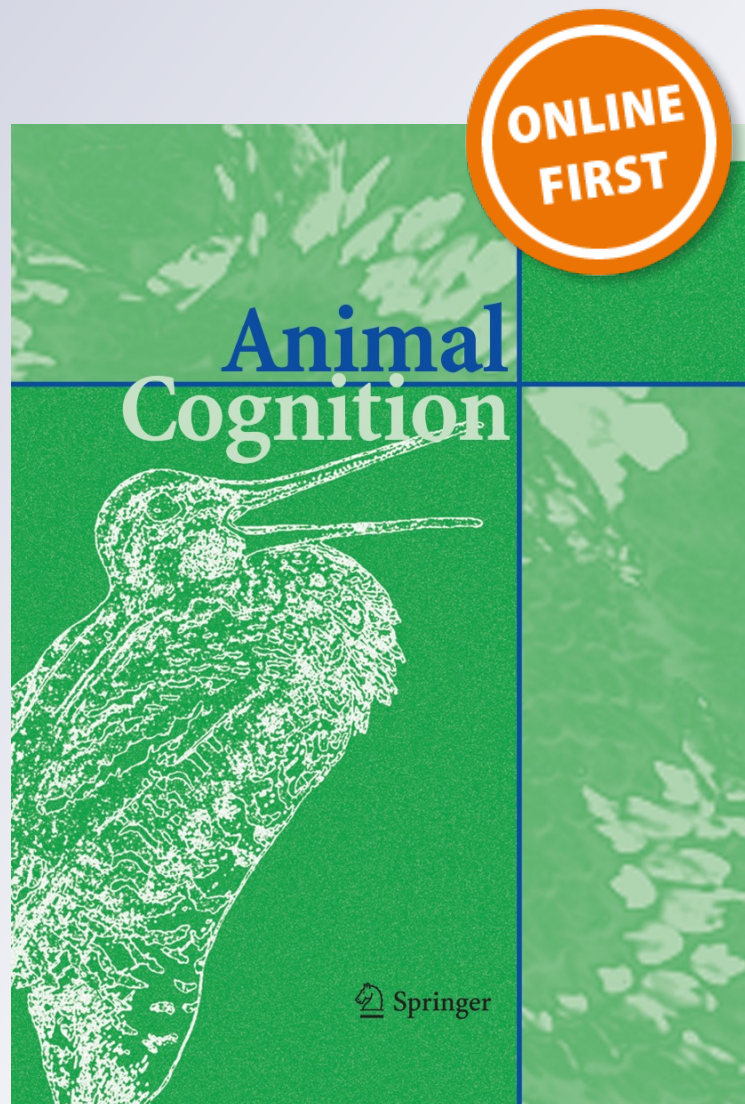
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The role of stimulus complexity, age and experience in the expression of exploratory behaviour in the Chimango Caracara, *Milvago chimango*

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Abstract Exploration represents an important way by which organisms evaluate environment information. The decision of whether or not an animal should investigate environmental changes may influence the extent to which animals learn about their surroundings and cope with habitat modifications. We analysed exploration behaviour in a suburban population of a raptor species, the Chimango Caracara, *Milvago chimango*, by examining how age, previous experience and object complexity influence novel object exploration. Our findings showed that object complexity did not influence caracaras initial approach and contact with objects, but did influence the degree of engagement during exploratory activities, as measured by total exploration time and number of exploration events. These variables were higher for complex objects than for simple objects. Experience resulted in less exploration of simple objects. It is likely that, for caracaras, simple objects are easier to encode and recall than complex objects, so additional exploration of such objects would not provide further information. Results suggest that exploratory behaviour in this raptor was guided more by the benefits of a greater quantity of information obtained by

exploring complex objects, than by the risks associated to this activity. We can conclude that caracaras cope with novel features in their surroundings with a novelty-seeking strategy, characteristic for generalist species in discovering early new resources opportunities, and which might be a determining factor for adaptive responses to environment modification.

Keywords Exploratory behaviour · Novelty · Stimulus complexity · Experience · Learning · *Milvago chimango*

Introduction

Exploratory behaviour represents an important way by which organisms gather information about the environment and learn its properties (Hughes 1997; Greenberg and Mettke-Hofmann 2001). Exploration in a wide sense encompasses any behaviour that results in the growth of knowledge. This implies that learning invariably occurs in any situation that evokes exploration (Welker 1961; Renner 1990), and which has vital influences on future decisions (Barnett 1958, 1963) possibly by establishing ‘cognitive maps’ to assist later searching behaviour (O’Keffe and Nadel 1978; Tolman 1948; Bell 1991). Novelty is one of the most important stimulus features capable of evoking and sustaining an exploratory response (Berlyne 1950; Hughes 1997). For this reason, the way in which an individual copes with novel features in its surroundings probably represents a decisive factor in their ability to respond adaptively to alterations occurring in their environment (Greenberg and Mettke-Hofmann 2001). Exploratory behaviour has also been used as a standard measure for quantifying variation in key ‘avian personality’ traits (Dingemanse et al. 2002; Réale et al. 2007) and

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has been shown to correlate with numerous other behavioural traits, such as boldness, aggression and dominance (Dingemanse and De Goede 2004 and references therein). Individual variation in these behavioural traits has been shown to have important fitness consequences and thus potentially underlie natural selection (Smith and Blumstein 2008).

Among species, the expression of exploratory behaviour varies with ecological requirements and habitat type (Mettke-Hofmann 2000; Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann et al. 2002). Individuals also show variability in their exploratory tendencies (i.e. Mettke-Hoffman et al. 2005, 2006; Biondi et al. 2010a, 2013), which may be modulated by intrinsic and extrinsic factors. For example, it is well known that the response to a novel stimulus is the result of interactions between an individual's internal response to novelty (i.e. intrinsic level of neophobia, Greenberg 2003) and previously acquired familiarity obtained during similar situations (Thorpe 1965; Heinrich et al. 1995). Therefore, prior experience is considered an intrinsic factor that can potentially determine the decision to explore, by influencing the level of uncertainties about a given situation, and the value of information that could be extracted from further exploration. In addition, particular attributes of the stimulus can considerably modify the exploratory response in animals (Berlyne 1950; Power 2000; Heyser and Chemo 2012). Complexity is one of the more important extrinsic factors that can influence exploration and so the manifestation of a neophobic response (Thorpe 1956; Hughes 1997; Power 2000). Complexity refers to the degree of diversity in the features present in a stimulus, which increases with the number of distinct elements and with size (Berlyne 1950; Greenberg 1983; Heinrich et al. 1995). Complex stimuli can elicit opposite reactions in an individual. On the one hand, more information can be extracted from more complex objects, which can lead to longer exploratory activities (Thorpe 1965; Jones et al. 1996). On the other hand, a complex stimulus may hide potential risks which can evoke a more intense neophobic response (Greenberg 1983; Mettke-Hofmann et al. 2006). A combined effect of these factors is also expected. In this sense, how complexity affected an individual's exploratory behaviour during a previous confrontation with a particular stimulus probably determines the influence that prior experience has on current decisions regarding exploration. For example, Jones et al. (1996) found that chicks (*Gallus gallus*) previously exposed to complex video images were still attracted to familiar complex images more than to unfamiliar simple ones during a posterior two-choice situation. Chicks that were exposed to simple images did not show any significant preference for either stimulus. Moreover, (Mettke-

Hofmann et al. 2006) working with garden warblers (*Sylvia borin*) found that groups of experienced and inexperienced birds had longer latencies to approach complex objects than simple ones, and experienced individuals took more time to approach either object type than inexperienced birds. That is, they observed an additive action of prior experience and object complexity on exploratory behaviour.

Cognitive research involving birds of prey is limited, despite findings that some species have a relative forebrain size comparable to those of parrots and corvids (Burish et al. 2004), and that some have also shown numerous feeding innovations (Nicolakakis and Lefebvre 2000; Lefebvre et al. 2001; Biondi et al. 2010a; Colbert-White et al. 2013). With reference to the analysis of novelty responses, little work has been done which included raptors as subjects (e.g. Negro et al. 1996; Beissinger et al. 1994; Biondi et al. 2010a, b, 2013). The Chimango Caracara (*M. chimango*, hereafter "caracara") is the most common Neotropical raptor over most of its range and one of the most abundant worldwide (Ferguson-Lees and Christie 2001). It is a generalist falconiform with a well-known ecological plasticity (Biondi et al. 2005) and gregarious habits (Ferguson-Lees and Christie 2001; Josens et al. 2013) that inhabits a broad range of habitat types and show a strong preference for human settlements (Ferguson-Lees and Christie 2001). Information about caracaras cognitive abilities has only recently become available through a series of studies (Biondi et al. 2008, 2010a, b, 2013). These studies have revealed that the caracara has a remarkable learning and innovative behavioural abilities and is also capable of transmitting novel behaviours through social learning. These previous analyses have also shown that these raptors exhibit highly variable exploratory responses, mainly among adult birds (Biondi et al. 2010a), which seem to vary significantly with the characteristics of the objects presented (Biondi et al. 2013). These observations led us to propose new experiments with the aim of analysing possible factors that modulate exploratory behaviour in this generalist predator. In particular, we report here the results of experiments conducted to evaluate the effect of age, stimulus complexity and experience on novel object exploratory response in caracara individuals, and to analyse how these factors interact during a subsequent exploratory situation. Since modifications in exploratory behaviour may influence directly what an individual learns about their surroundings, investigating the key factors that promote exploration in caracaras can lead to a better understanding about how differences in learning may affect their ability to adapt to novel and changing environmental conditions, such as urban settings (Mettke-Hofmann et al. 2006; Brown 2012).

Methods

Subjects and housing

Thirty-one adult birds and 30 juveniles (under 1-year old) were caught with baited walk-in traps (Bloom 1987) in a suburban area within Mar del Plata city, Argentina (7,950 ha, and half a million inhabitants) between March and August (non-breeding period) of 2010 and 2011. We used plumage colour (mainly tail feathers), tarsus colour and moult stage to determine age (White et al. 1994; Ferguson-Lees and Christie 2001). Birds were identified with leg bands, weigh after capture and then housed in individual outdoor aviaries ($2 \times 1.5 \times 1.5$ m) following housing and care conditions described by Bloom (1987), Aprile and Bertonatti (1996). Aviaries were visually isolated from one another by black synthetic fabric, ensuring that individuals performed on their own, without social motivation (Biondi et al. 2008, 2010a, 2013). To become habituated to captivity, birds were given a one-week period during which they were fed once a day from a dish containing beef and chicken meat and water was provided *ad libitum* (Biondi et al. 2008). All individuals were naïve at the beginning of the two experiments and were released at their capture sites at the end of the experimental tests.

Experimental procedure

After the habituation period, we performed two separate experiments (see below) on separate groups of individuals. All birds were always fed at 9:00 a.m. with 60 g of food (Bloom 1987; Biondi et al. 2008). After the habituation period the birds always finished the entire amount of food given. Experiments were performed at least 1 h after feeding was complete. We continuously filmed each trial using a Sony HD camcorder, located at 10 metres from the aviaries, using zoom to avoid any interference from the camera.

Experiment 1

We examined the effect of object complexity on exploratory behaviour and whether age had any effect on exploration. The experiment was performed on 39 individuals (20 adults and 19 juveniles) with one group (12 adults and 9 juveniles) exposed to three simple objects simultaneously and the remainder (8 adults and 10 juveniles) exposed to three complex objects during a single 25-min trial. Simple objects had geometric shapes (e.g. cross, square and circle) of two dimensions and were made of plastic material without irregularities, volume, holes or salient elements. Complex objects were a combination of

two three-dimensional geometric elements (e.g. an open cube glued to a cylindrical base) with concavities and protruding elements (Fig. 1). The diameters of the two object groups were about 10 cm. All objects were of plastic material in three different colours (e.g. yellow, red and blue). One object of each different colour was always presented in each trial. We recorded the time that elapsed from introduction of the objects until the individual's first approach to within 10 cm as a measure of approach latency, and the time from this first approach to first contact as a measure of contact latency; in addition, we recorded the number of objects explored, the number of exploration events and the total exploration time. Each exploration 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.

Experiment 2

We assessed here how prior experience influenced the potential effect of object complexity on exploratory behaviour of adults and juvenile birds. We conducted this experiment with two groups of 22 individuals each (11 adults and 11 juveniles), which were different to those used in Experiment 1. These groups were exposed to different treatments before the final exploration test—the experimental group was given previous experience with simple and complex objects, while the control group was not. We presented each individual of the experienced group with three objects, simultaneously, in two separate 25-min trials (10:00–11:00 and 14:00–15:00) during three consecutive session days (labelled S1–S3). During the initial trial in the first session, (S1) 12 individuals (6 adults and 6 juveniles) were exposed to complex objects and 10 individuals (5 adults and 5 juveniles) to simple objects. The opposite order was used in the second trial on the same day. We continued using the same protocol for the remaining sessions, though we randomized the order of presentation of both type of objects. The simple and complex objects were the same as in Experiment 1. Individuals of the control group were not provided with any object during the three session days, but were fed at the same hour as the other birds, and were approached by the researcher at the same times as when the two trials started for the experimental group. The exploration test (labelled S4) was performed 5 days after completing the treatment. This test consisted of a single 25-min trial during which individuals from both experienced and control groups were exposed to three simple or complex objects. Half the individuals of each group were presented with simple objects and the other half with complex ones. Individuals were randomly exposed to one or another object type. We used identical objects to

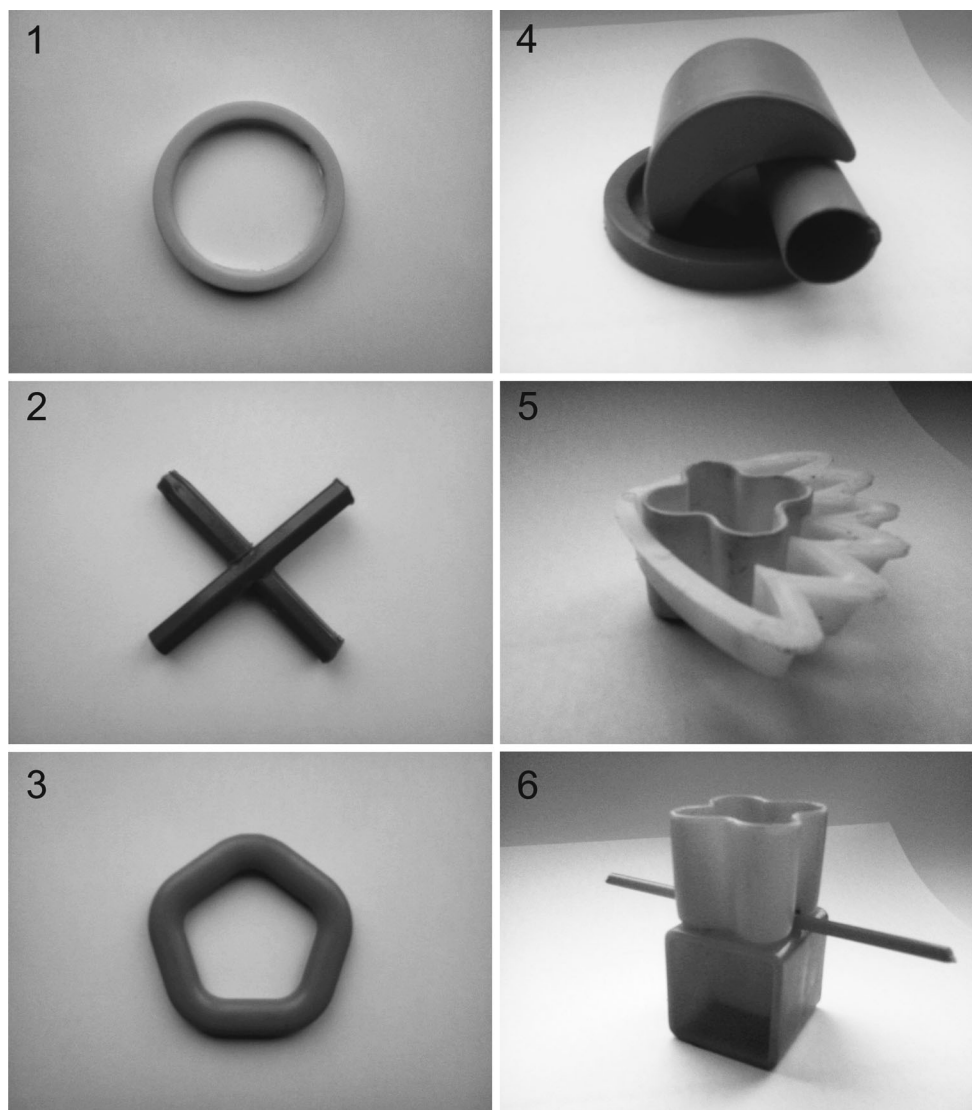


Fig. 1 Picture showing the simple (1–3) and complex objects (4–6) used during the experiments

those used in treatment sessions. The behavioural variables recorded were the same as in Experiment 1.

Data analysis

We assessed the effect of object complexity, age and experience on exploratory behaviour using generalized linear models (GzLM). The response variables considered were approach and contact latencies, total exploration time, number of exploratory events and quantity of objects explored. We used Gamma error structure and inverse link function to analyse the time-related variables and Poisson error structure with log-link function for number of events and objects (Crawley 2007). For Experiment 1, predictor variables included age (adult-juvenile) and object type (simple-complex). For Experiment 2, we performed a GzLM to evaluate the effect of interaction among

experience and object complexity on exploration. In the model, we included treatment (experimental vs. control), object type (complex vs. simple) as factors, and contact latency, exploration time and number of exploration events, as response variables. We performed a separate analysis for each age class. According to a previous study, caracara exploratory behaviour is not influenced by sex (Biondi et al. 2013), so we excluded this factor from the behavioural analysis.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate support for models with all possible combinations of predictor variables, including a global model with all predictors and their interactions, as well as a null model without predictors. Model selection was performed using the MuMIn-R package (version 1.9.13.), and based on Akaike's information criterion corrected for lack of independence and small sample sizes

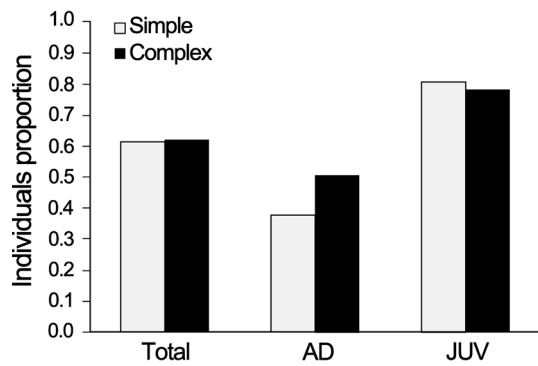


Fig. 2 Proportion of caracara individuals that showed exploratory behaviour when confronted with simple and complex objects in Experiment 1. Results are shown for all individuals (Total) and for adults (AD) and juveniles (JUV) separately

(AICc; Burnham and Anderson 2002). We used two measures to provide further insight into the amount of uncertainty in model selection. The first was the difference in AICc between the best approximating model and all the other models (Burnham and Anderson 2002), termed $\Delta AICc$. In general, an AICc score between 0 and 2 indicates substantial support for the model (Burnham and Anderson 2002). The second measure calibrates models to provide relative plausibility by normalizing each model on the basis of its $\Delta AICc$ value, termed “model weight” (Anderson and Burnham 1999; Burnham and Anderson 2002). To evaluate the support for predictor variables, parameter likelihood was estimated (Burnham and Anderson 2002); predictor variables with good support will have high parameter likelihood values (near 1). Parameter estimates were calculated by the technique of model averaging (model-averaged inference) from AICc weights for all candidate models (Burnham and Anderson 1998). Unconditional variances of those candidate models were used to calculate standard errors. To supplement evidence of important effects with parameter likelihoods, we also assessed the degree to which 95 % confidence intervals of parameter estimates overlapped zero. We calculated upper and lower confidence limits by adding or subtracting $2 \pm SE$, respectively. All statistical analyses were carried out using R software, version 3.0.2 (R Development Core Team 2013).

Results

Experiment 1

Sixty-two per cent of individuals contacted at least one object during Experiment 1. A higher proportion of juveniles (79 %) compared to adults (40 %) explored the objects ($\chi^2 = 4.6, df = 1, P = 0.032$). The proportion of

Table 1 Results from the generalized linear models showing the factors that affect the exploration variables analysed during the experiment 1

Responses	Models	Factors	K	$\Delta AICc$	AICc weight	R^2
Contact latency	1	Age	3	0.00	0.62	0.17
	2	Age + type	4	1.81	0.25	0.18
	4	Null	2	6.97	0.02	–
Exploration time	1	Age + type	4	0.00	0.74	0.37
	2	Age \times type	5	2.22	0.24	0.39
	5	Null	2	18.70	0.00	–
Events	1	Age + type	4	0.00	0.77	0.48
	2	Age \times type	5	2.46	0.23	0.49
	5	Null	1	77.71	0.00	–
Objects	1	Age + type	4	0.00	0.58	0.22
	2	Age	3	1.88	0.23	0.17
	4	Null	1	15.92	0.00	–

Number of parameters (K) in each model included the intercept and each explanatory variable. Only models with greatest support are shown (i.e. $AICc < 3$)

birds that showed exploratory behaviour when confronted with simple objects (62 %) was similar to that proportion observed exploring complex ones (61 %) ($\chi^2 = 0, df = 1, P = 1$). This pattern persisted even when adults ($\chi^2 = 0.01, df = 1, P = 0.92$) and juveniles ($\chi^2 = 0, df = 1, P = 1$) were analysed separately (Fig. 2).

All individual that approached objects also contacted them. Since these two variables were highly correlated ($r = 0.97, N = 39, P < 0.001$) for further analyses, we used only contact latency. Results show that age class was the strongest variable explaining contact latencies variation in our model (Table 1). The importance of this variable is also indicated by the high parameter likelihood (≈ 1) and by the fact that it was the only variable whose confidence interval did not include 0 (Table 2). Juveniles were quicker than adults in contacting objects for the first time (Table 2). Total exploration time was explained mainly by age class and object type (Table 1; Fig. 3a). This model accounted for 74 % of the response variation. As can be seen in Table 2, juveniles explored longer than adults. Also, both adult and juvenile individuals presented with complex objects explored longer than those confronted with simple ones (Fig. 3a; Table 2). The number of exploratory events was also mostly explained by age class and object type (Table 1; Fig. 3b). Juveniles performed more events than adults, and both age classes performed a greater number of events on complex objects than on simple ones (Fig. 3b; Table 2). The number of objects contacted was similar during exploration of both simple and complex objects but higher for juveniles than adult birds (Table 1, 2).

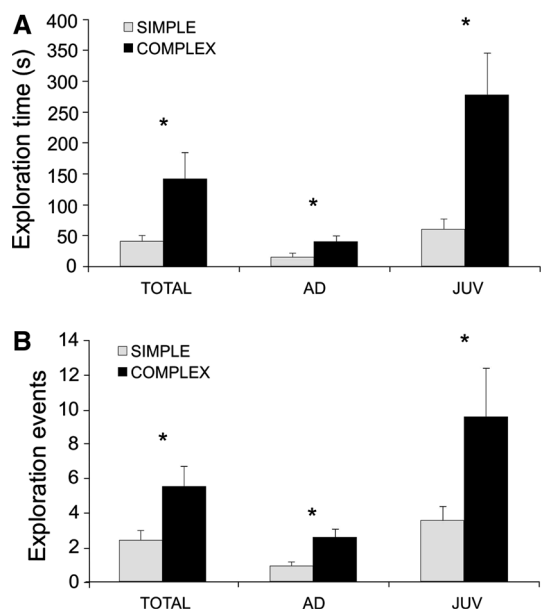


Fig. 3 Mean ± SE values of exploration time (a) and exploration events (b), shown by caracara individuals on simple and complex objects during Experiment 1. Values are given for all individuals (Total) and for adults (AD) and juveniles (JUV) separately. Asterisk indicates significant differences (CI without including zero) in the response variable values between simple and complex object presentations

Experiment 2

The overall percentage of individuals that explored at least one object during the exploration test (S4) was similar between control (70 %) and experimental (60 %) groups ($\chi^2 = 0.11, df = 1, P = 0.746$). This pattern was observed even after data for adults (experienced: 50 %; control 60 %; $\chi^2 = 0.18, df = 1, P = 0.668$) and juveniles (experienced: 50 %; control: 60 %; $\chi^2 = 0, df = 1, P = 1$) were separated. Within the control group the percentage of individuals that showed exploration during S4 was similar for those exposed to either simple (70 %) or complex objects (80 %) ($X\text{-squared} = 0, df = 1, P = 1$; Fig. 4a). Within the experienced group, however, the percentage showing exploration during S4 was higher in those confronted with complex objects (90 %) than with simple objects (40 %) ($\chi^2 = 4.91, df = 1, P = 0.027$; Fig. 4b). This difference was particularly notable in adults, even though it was not enough to show statistically significant differences for either age classes (Juveniles: $\chi^2 = 0.41, df = 1, P = 0.521$; adults: $\chi^2 = 0.88, df = 1, P = 0.347$).

Once again, all individuals that approached objects also contacted at least one of them and, since these two variables were highly correlated ($r = 0.96, N = 32, P < 0.001$), we directly analysed contact latency as in Experiment 1.

Table 2 Parameter estimates (±SE) from generalized linear models (GLMs) describing the factors affecting the exploratory behaviour during experiment 1

Responses	Factors	Parameter likelihood	Categories	Par. est. ± SE	CI
Contact latency	Intercept			6.51 ± 0.46	5.57:7.45
	Age	0.99	Juvenile	-1.29 ± 0.63	-2.57:-0.02
	Type	0.26	Simple	0.34 ± 0.59	-0.87:1.55
	Age: type	0.12	Juvenile:simple	-0.85 ± 1.22	-3.34:1.62
Exploration time	Intercept			3.77 ± 0.27	3.22:4.34
	Age	1.00	Juvenile	1.75 ± 0.37	1.01:2.49
	Type	0.74	Simple	-1.26 ± 0.33	-1.93:-0.59
	Age: type	0.24	Juvenile:simple	-0.48 ± 0.63	-1.77:0.79
			ad:sim vs. com*	-1.02 ± 0.44	-1.93:-0.12
			juv:sim vs. com*	-1.51 ± 0.45	-2.42:-0.60
Events	Intercept			0.96 ± 0.17	0.61:1.30
	Age	1.00	Juvenile	1.29 ± 0.19	0.90:1.69
	Type	1.00	Simple	-1.00 ± 0.23	-1.50:-0.49
	Age: type	0.22	Juvenile:simple	0.03 ± 0.44	-0.87:0.92
			ad:sim vs. com*	-0.56 ± 0.58	-1.72:-0.61
		juv:sim vs. com*	-0.94 ± 0.39	-1.75:-0.14	
Objects	Intercept			-0.46 ± 0.33	-1.14:0.21
	Age	1.00	Juvenile	1.76 ± 0.49	0.74:2.77
	Type	0.65	Simple	-0.80 ± 0.47	-1.77:0.16
	Age: type	0.32	Juvenile:simple	-0.43 ± 0.85	-2.15:1.30

Parameter likelihoods are indicative of the importance of the explanatory variable. Confidence intervals (95 %) were calculated adding or subtracting 2 SE
 Bold identifies significant terms (CI not including zero)
 * Indicates contrasted levels within each age classes

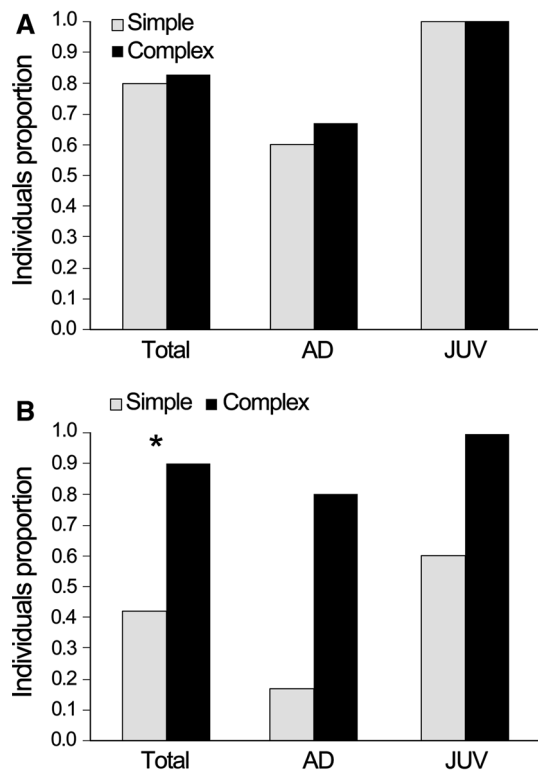


Fig. 4 Proportion of caracara individuals within control group (a) and experience group (b) that showed exploratory behaviour when confronted with simple and complex objects in Experiment 2. Proportions calculated for all individuals (Total), as well as for adults (AD) and juveniles (JUV) separately. Asterisk identifies significant differences, $P < 0.05$

Previous studies of this species (Biondi et al. 2010a, b, 2013), along with the results from Experiment 1, showed that adults and juveniles differed in all exploratory behaviour variables. Consequently, we performed separate analyses for the two age classes. During the exploration test (S4), adult contact latencies were not significantly explained by any factor (Table 3). However, juveniles' contact latencies were best explained by the interaction of treatment and object type (Table 3). Complex objects were contacted faster than simple ones, though this tendency was only statistically significant for the juveniles belonging to the experimental group (Table 4). Analysis also showed that only for simple objects did the experimental group show higher contact latencies than the control group (Fig. 5a).

In adults, the total exploration time was best explained by object type and its interaction with treatment (Table 3). The same explanation applies to the number of exploration events. In the two cases, the best model explained only 22 and 26 % of the variation, respectively. As it can be deduced from the confidence intervals (Table 4), exploration time and number of events in adults were higher for complex objects than for simple objects, and this pattern was especially true for individuals coming from the

Table 3 Generalized linear models explaining object type and treatment effects on exploration variables during experiment 2 for adults (a) and juveniles (b)

Response	Models	Factors	K	$\Delta AICc$	AICc	R ² weight
(a) Adults						
Contact latency	1	(Null)	2	0.00	0.48	–
	2	Type	3	1.11	0.28	0.05
	3	Trat	3	2.23	0.16	0.01
Exploration time	1	Type	3	0	0.54	0.22
	2	Trat:type	5	1.64	0.24	0.34
	3	Trat + type	4	2.52	0.15	0.24
	4	(Null)	2	4.65	0.05	–
Events	1	Type	2	0.00	0.54	0.26
	2	Trat:type	4	1.03	0.32	0.34
	3	Trat + type	3	2.69	0.14	0.25
	4	(Null)	1	13.06	0.00	–
(b) Juveniles						
Contact latency	1	Trat:type	5	0.00	0.63	0.51
	2	Type	3	2.09	0.22	0.33
	5	Null	2	10.61	0.00	–
Exploration time	1	Trat:type	5	0.00	0.65	0.69
	2	Trat + type	4	1.43	0.32	0.62
	4	(Null)	2	10.61	0.00	–
Events	1	Trat:type	4	0.00	0.81	0.59
	5	(Null)	1	58.16	0.00	–

Number of parameters (K) in each model included the intercept and each explanatory variable. Only the models with greatest support (i.e. $AICc < 3$), as well as the Null model, are shown

experience group. Moreover, only for simple objects did, we observe a significant difference between treatments with both response variables being lower in the experimental group than among control individuals (Fig. 5b, c).

For juveniles, interaction between treatment and object type provided the best models to explain the exploration time and events variability in the analysis (Table 3). This model explained 69 and 59 % of the variation, respectively. Overall, both variables were higher for complex objects than for simple objects (Table 4), and this difference was significant in both control and experimental groups (CI not including 0, Table 4). For adults, differences between treatment groups existed only for simple objects, with experienced individuals exploring less and performing fewer events on simple objects when compared to control birds (Table 4; Fig. 5b, c).

Discussion

In this study, the effects of stimulus complexity and individual experience on object exploration were analysed for

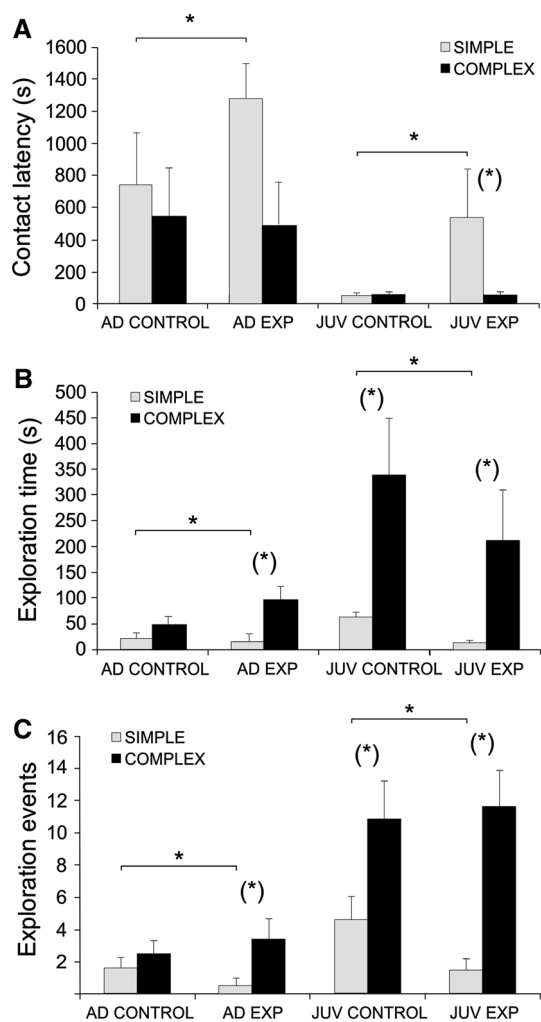


Fig. 5 Comparison of contact latency (a), exploration times (b) and exploration events (c) between simple and complex objects by adults and juvenile caracaras from control and experimental groups, during Experiment 2. (Asterisk) indicates statistically significant contrasts (CI not including zero) in response variables. Horizontal bars with an asterisk identify statistically significant contrasts between control and experimental treatment

individuals of the Chimango Caracara, *M. chimango*, taking into account the possible effect of age. In general terms, our findings showed that in this raptor the bird's age—but not the object's structural complexity—affected the initial decision to explore, as measured by proportion of individuals that did explore, and by the time until first contact of novel objects. Nevertheless, complex objects seemed to stimulate longer and deeper exploration than simple ones, both for adults and juveniles. Birds with experience showed less exploratory behaviour when simple objects were available, and this pattern was particularly notorious in adult birds.

It has been observed that juvenile birds are more commonly attracted to approach and manipulate objects, and this tendency is less prone to habituation in them than in

adult birds (Marchetti and Price 1989; Vince 1960; Greenberg and Mettke-Hofmann 2001; Power 2000). Indeed, previous studies on the exploratory behaviour of caracaras of natural and artificial objects have shown that young birds were more quickly attracted to novel objects presented in a familiar context, and performed more persistent and longer explorations than adult raptors (Biondi et al. 2010a, 2013). We also found this to be true. Compared with adult birds, more juveniles explored objects, both complex and simple, and explored for longer periods with a greater number of exploration events. This pattern appears in most studies comparing exploratory and play behaviour between age groups and has been related to the high information benefits for inexperienced juveniles during exploration and to the possibility of learning during object manipulation and play (Power 2000; Biondi et al. 2013).

Physical properties of a stimulus, such as colour, size or structural complexity, have been observed to influence the investigation of an object (Berlyne 1950; Weisler and McCall 1976; Mettke-Hofmann et al. 2006). Studies like those carried out by Mettke-Hofmann et al. (2006) on garden warblers have shown that birds take more time to approach and contact complex objects than to approach simple ones, which was assumed to be because individuals are influenced more by the risks associated with exploring a novel situation (i.e. risk-aversion or neophobia) than by its benefits (i.e. novelty-seeking or neophilia). Additionally, other studies have found that more complex elements elicited longer exploration than less complex ones (Berlyne 1950; Thorpe 1956; Jones et al. 1996; Biondi et al. 2013). At first glance, from the results of Experiment 1 in this study, the initial decision to explore was influenced by the presentation of the novel objects itself, but not by its structural properties. A similar proportion of individuals explored both complex and simple objects, and there was no difference in the time until first contact between these two object types. However, complexity did influence the degree of engagement during exploratory behaviour shown by individuals. Thus, a complex design promoted longer and more persistent investigation of the objects than a simple one. In the light of these findings, we suggest that caracara exploratory behaviour is guided more by the quantity of information that could be extracted from objects than by the potential risks that could be associated to their exploration.

It may well be that longer exploration of complex objects helped birds inspect thoroughly not only the surface but also its content. These observations may also be explained through objects' functional properties or affordances (Chemero and Heyser 2005). As defined by some authors, affordances are considered a means of connecting perception directly with behaviour (Chemero 2003, 2009;

Table 4 Parameter estimates (\pm SE) from generalized linear models (GLMs) describing the factors affecting the exploratory behaviour, during experiment 2 for adults and juveniles, separately

Variables		Par. Likelih.		Contrast levels	Par. est. \pm SE		CI		
Response	Factors	AD	JUV		AD	JUV	AD	JUV	
Contact latency	Type	0.36	0.97	Simple	0.6 \pm 0.4	1.7 \pm 0.6	-0.24:1.57	0.38:3.06	
	Trat	0.23	0.14	Exp	0.3 \pm 0.5	-0.2 \pm 0.9	-0.65:1.25	-1.99:1.53	
	Trat \times type	Simple:exp	0.01	0.63	Simple:exp	0.6 \pm 0.9	2.4 \pm 0.9	-1.30:2.52	0.45:4.42
		Control:simple ^a			Control:simple ^a	0.3 \pm 0.7	0.2 \pm 0.8	-1.04:1.67	-1.19:1.61
		Exp:simple ^a			Exp:simple ^a	0.9 \pm 0.7	2.7 \pm 0.7	-0.43:2.28	1.24:4.05
		Simple:exp ^b			Simple:exp ^b	0.5 \pm 0.6	1.9 \pm 0.6	-0.82:1.88	0.55:3.36
		Complex:exp ^b			Complex:exp ^b	-0.1 \pm 0.6	-0.4 \pm 0.6	-1.44:1.27	-1.88:0.92
Exploration time	Type	0.93	1.00	Simple	-1.7 \pm 0.5	-2.4 \pm 0.4	-2.78:-0.73	-3.13:-1.61	
	Trat	0.17	0.65	Exp	0.3 \pm 0.8	-0.6 \pm 0.5	-1.49:1.99	-1.75:0.51	
	Trat \times type	Simple:exp	0.24	0.32	Simple:exp	-2.3 \pm 1.1	-1.4 \pm 0.6	-4.50:-0.06	-2.84:-0.08
		Control:simple ^a			Control:simple ^a	-0.8 \pm 0.7	-1.7 \pm 0.4	-2.33:0.80	-2.64:-0.68
		Exp:simple ^a			Exp:simple ^a	-3.1 \pm 0.7	-3.2 \pm 0.5	-4.62:-1.48	-4.11:-2.15
		Simple:exp ^b			Simple:exp ^b	-1.6 \pm 0.8	-1.8 \pm 0.5	-3.15:-0.02	-2.82:-0.86
		Complex:exp ^b			Complex:exp ^b	0.7 \pm 0.8	-0.4 \pm 0.5	-0.87:2.27	-1.36:0.59
Events	Type	1.00	0.87	Simple	-1.3 \pm 0.4	-1.3 \pm 0.9	-2.15:-0.05	-1.75:-0.92	
	Trat	0.14	0.81	Exp	0.2 \pm 0.3	0.1 \pm 0.2	-0.56:0.96	-0.34:0.44	
	Trat \times type	Simple:exp	0.32	0.19	Simple:exp	-1.7 \pm 0.7	-1.2 \pm 0.4	-3.05:-0.09	-2.09:-0.27
		Control:simple ^a			Control:simple ^a	-0.6 \pm 0.5	-0.8 \pm 0.2	-1.60:0.31	-1.36:-0.34
		Exp:simple ^a			Exp:simple ^a	-2.4 \pm 0.7	-2.1 \pm 0.3	-3.94:-0.81	-2.79:-1.29
		Simple:exp ^b			Simple:exp ^b	-1.4 \pm 0.8	-1.1 \pm 0.4	-3.11:-0.04	-1.94:-0.29
		Complex:exp ^b			Complex:exp ^b	0.3 \pm 0.3	0.1 \pm 0.1	-0.42:1.02	-0.51:0.17

Parameter likelihoods are indicative of the importance of the explanatory variable. Confidence intervals (CI 95 %) were calculated adding or subtracting 2 SE

Bold identifies significant terms (CI not including zero)

^a Contrasted levels as object type, performed within each treatment group

^b Contrasted levels as treatment performed within each object type

Michaels 2003; Turvey et al. 1992) and relate an animal's abilities with some aspect of the environment or object that enables behaviour. For example, adult mice (*Mus musculus*) confronted with two objects that differed in their affordances—one could only be touched and the other could also be climbed—explored objects that can be climbed more than objects that can only be touched, but more quickly showed habituation to objects that could only be touched (Heyser and Chemero 2012). These results paralleled with those in our work in that the complex objects could be used and manipulated in more diverse ways than the simple elements, so leading to longer and deeply exploration. Similar results were also found in a previous study of caracaras in which birds showed greater preference and performed more manipulative actions—some of which similar to those categorized as play behaviours—over two unique elements in a set of natural and artificial objects that presented shapes with conspicuous volume and concavities (Biondi et al. 2013).

Prior experience can reduce uncertainty during similar subsequent situations (i.e. throughout stimulus generalization). This, in turn, may affect the value of information extracted, influencing whether to engage in exploration (Inglis 2000; Inglis et al. 2001). Thus, through the habituation process, repeated exposure to an object may reduce exploration (i.e. leading to less time exploring) as well as avoidance (i.e. decrease of approach latencies), as has been shown in several studies of birds (Heinrich et al. 1995; Greenberg and Mettke-Hofmann 2001) and mammals (Renner and Seltzer 1991; Poucet et al. 1988). Overall, in this study, experience seemed to reduce exploration most when simple objects were presented. First of all, the number of experienced individuals that contacted objects during the exploration test was lower when presented with simple objects than with complex objects, whereas in the control group there was little difference, especially for adult birds. In line with these observations, adults of the experienced group explored complex objects for much

longer than they did with simple objects. Control adults, on the other hand, expended similar exploration times and performed a similar number of events towards both object types.

Moreover, individuals in the experienced group that were confronted with simple objects during the exploration test showed lower exploration time and fewer exploration events compared to control birds also exposed to simple objects. However, birds in both control and experience groups showed similar time and quantity of exploration events on complex objects. Thus, experienced birds continued to be highly attracted to complex objects despite the fact that they had been exposed to them some days before. Persistence in investigating elements with which individuals had prior experience might reflect the continued need for updating information on these objects because their structural complexity may include features or resources that they had not previously discovered. Alternatively, it is well known that when birds have habituated to an object's presence, after the object has not been encountered again for a period of time, latency to approach it may rebound to high levels (Thorpe 1956). For example, in wood warbler individuals previously familiarized with a novel object located next to the food, a substantial recovery of the original feeding latencies occurred after non-exposure of the object for 1 week (Greenberg and Mettke-Hofmann 2001). In our work, after non-exposure of objects for 5 days, experienced individuals explored with similar latencies and intensities as control individuals only when complex objects were presented. It is possible that, because of this complexity, individuals failed to successfully retrieve information gained during their prior experience so as to recognize them as already known objects. Therefore, these later presentations might be perceived as a novel scenario for both age classes. In this sense, complex forms such as those objects used in this study are made up of a collection of shape features which would imply that remembering these objects involves encoding and the retention of several features conjunctions. Memory for such stimuli has been shown to be a particularly demanding process (Wheeler and Treisman 2002; Luria et al. 2009). These results also suggest that, at least for complex objects, some continued exposure may be necessary to maintain familiarity and, consequently, an object's status.

Summarizing, this work provides new information about factors that promote and modulate exploratory behaviour in a generalist bird of prey, the Chimango Caracara. This raptor is a highly exploratory species, which investigates new stimuli not only because of their novelty, but also due to the amount of potential information that could be extracted. This, in turn, promotes a high intensity and persistence of exploratory behaviour by both adults and juveniles. That is, caracara individuals cope with novel

features of their surrounding with a novelty-seeking strategy. Generalist predators, like caracaras, showing few morphological or behavioural specializations for a particular mode of foraging (Biondi et al. 2005; Biondi 2010), can exploit a broad range of food types and foraging sites, and therefore is advantageous for them to show strong exploratory tendencies (Greenberg 1983). Especially for those caracara individuals which inhabit areas like urban settings, with high diversity of anthropogenic novel stimuli, this characteristic can be critical for quickly discovering new resource opportunities and for learning about their value, which might be a decisive factor for their ability to respond adaptively to continue environment modifications.

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