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Brief communication

Visual acuity in an opportunistic raptor, the chimango caracara (*Milvago chimango*)



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HIGHLIGHTS

- We estimated the visual acuity of the chimango caracara using operant conditioning experiments
- Chimango caracara visual acuity ranges from 15.08 to 39.83 c/deg
- Chimango caracaras have the lowest visual acuity estimated in any raptor to date
- Their relatively lower visual acuity may reflect their foraging on the ground

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ABSTRACT

Raptors are always considered to have an extraordinary resolving power of their eyes (high visual acuity). Nevertheless, raptors differ in their diet and foraging tactics, which could lead to large differences in visual acuity. The visual acuity of an opportunist bird of prey, the Chimango caracara (*Milvago chimango*) was estimated by operant conditioning. Three birds were trained to discriminate two stimuli, a positive grey uniform pattern and a negative grating pattern stimulus. The visual acuity range from 15.08 to 39.83 cycles/degrees. When compared to other birds, they have a higher visual acuity than non-raptorial birds, but they have the lowest visual acuity found in bird of prey so far. We discuss this result in the context of the ecology of the bird, with special focus on its foraging tactic.

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1. Introduction

Among vertebrates, birds are certainly the most dependent on vision [1] although some groups, like procellariiforms and vultures may use olfaction more than previously recognized [2, 3]. Visual acuity is one of the most frequent parameters that has been studied in bird vision and many studies assessed visual acuity using operant conditioning experiments in various species ranging from passerines [4, 5] to raptors [6–8]. The eyes of diurnal raptors are often considered to afford elevated spatial resolving power, yet only few species have been extensively studied: the wedge-tailed eagle (*Aquila audax*), the brown falcon (*Falco berigora*), the American kestrel (*Falco sparverius*) and some vulture species [6, 7, 9–11]. Although visual acuity in the wedge-tailed eagle is the highest estimated in vertebrate to date, we cannot generalize these findings to all raptors. Raptors differ highly in their ecology: some are exclusive predators, others are scavengers or opportunists [12]. Because diet and foraging represent important factors that influence spatial resolving

power in a given species (e.g. active predators have higher visual acuity than herbivores among mammals) [13], raptors with different diets may thus have different resolving power.

Here, we estimated the visual acuity of an opportunistic species, the chimango caracara *Milvago chimango* (order falconiformes). In contrast to eagles, falcons and vultures that search for food in flight, chimango caracaras are opportunists in their feeding behavior and mainly forage on the ground [12]. This would suggest that they might have high visual acuity to search for small moving prey, but probably lower than predatory birds such as eagles or falcons that search for prey from a perch or in flight.

2. Methods

2.1. Animals

The three captive born chimango caracaras used in this study were living in individual aviaries (dimensions 4 × 4 × 3 m high) at the falconry park “le Rocher des Aigles”, France (44°48′4″N, 1°36′55″E). Birds were weighed every day and were maintained at approximately

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90% of their free feeding weights during the experiment (see Table 1). Because these birds are usually used in a flight show (except during the experiment), all had previous experience of operant conditioning.

2.2. Experimental aviary and experimental device

The trial aviary (8 × 20 m in area and 6 m high) was located outdoors and covered with a net. A starting perch was placed at 10 m distance from two wooden boxes (6 m from each other), in which two monitors (Samsung S22C300H) were placed to present the visual stimuli (created on R.3.1.2 (R Development Core Team 2014) and presented on PowerPoint 2010). Monitor sizes were 510 × 398 mm that correspond to 2.92 × 2.28° of visual angle for the birds at 10 m. The two boxes were 70 cm wide, 80 cm high and 120 cm long and painted in black to create a “dark room”, in order to avoid any effect of direct sunlight on the screens. The luminance in the two boxes while screens were turned off was measured for each test phase and was not different between the two boxes (Left box: 115.63 ± 8.57 Lux; right box: 109.08 ± 10.59 Lux, *t*-test, *t* = 0.48, *df* = 44.07, *p* = 0.63). A feeding box with ten compartments and a perch was placed below each box with the screens. Each compartment contained a piece of chicken meat as a reward. To avoid any effect of possible olfactory cues, each compartment was perforated. When a bird made a correct choice, the observer (S.P.) opened a compartment from a distance using electric motor with a switch.

2.3. Assessment of visual acuity

Before each experiment, we ensured that the cage was oriented in such way that birds never had to fly against the sun. The birds were trained to fly towards one of the screens and to choose between a negative stimulus (composed of black and white stripes) and a positive stimulus (uniform grey). The grey stimulus was either slightly darker (10%) or slightly brighter (10%) than the pattern to make sure the birds could not use brightness as a cue. The birds indicated a choice by flying to one of the two perches below the monitors. The determination of visual acuity involved two phases.

Phase 1 (training): the birds had to learn to fly from the starting perch to the uniform stimulus while the other monitor presented a coarse grating (1.71 cycles per degree, abbreviated c/deg). During the first two days, the feeding boxes were presented to the birds to ensure that they could see into the compartments. This step was necessary to train the birds to fly to the perch. Later, the food was hidden. During the training phase, the monitors were switched off after 5 s if the bird made an incorrect choice, and after the bird had finished eating if the birds made a correct choice. Two sessions of 30 trials were conducted every day. For each trial, if the bird made a correct choice, one compartment was opened and the bird received a reward (3 g of chicken meat). For a session of 30 trials, gratings and uniform greys were presented 15 times, on each side, while the side of the stimulus was changed in quasi-random order. To prevent side preferences, the positive stimulus was presented on the same side for a maximum of three consecutive trials [6].

Phase 2 (Test): when the bird made more than 80% of correct choice during 3 consecutive training sessions, the test phase could begin. Two sessions were conducted per day. Before each test session, we presented 5 coarse gratings to ensure that the birds were still conditioned to the grey pattern. We conducted 5 sessions of 30 trials and 3 sessions of 28

trials, with 9 different gratings (1.71, 9.59, 17.98, 20.55, 23.97, 28.77, 41.10, 47.95 and 143.84 cycles per degree) that were presented randomly across trials and sessions. Each grating was presented 26 times. When the birds were about to leave the starting perch, the monitors were switched off to ensure that they could not alter their decision on the way. The observer (S.P.) was hiding in a cabin to avoid any bias to the choice of the bird but he was not blind of the experiment in order to open a box compartment with a reward if the birds made a correct choice.

2.4. Eye size

Corneal diameters were measured with ImageJ 1.49 from close-up photographs of the three individuals, according to [14]. The mean corneal diameter (CD, in mm) for each species was translated to axial length (AL), using the formula [15] for diurnal animals:

$$AL = CD/10^{-0.22} \quad (1)$$

We then calculated the visual acuity (VA) using the allometric function [16]

$$VA = 10^{(1.42 \times \log_{10}(AL) - 0.11)} \quad (2)$$

We compared the visual acuity obtained by the allometric function with the visual acuity obtained by operant conditioning experiment.

2.5. Data analysis

Analyses of behavioral data were performed with R.3.1.2 (R Development Core Team 2014) using psyphy [17] and ggplot2 [18] packages. To determine the threshold of visual acuity (72.5% correct choices, binomial test, *n* = 26, *p* < 0.05), we fitted a psychometric function for each individual using a generalized linear model (GLM).

3. Results

The visual acuity of three chimango caracaras assessed by operant conditioning ranged from 15.08 to 39.83 c/deg (Fig. 1, Table 1). Individuals differed in their ability to learn the task. Especially, the individual (Flow) showing the lowest value of visual acuity needed twice as much time to be conditioned to the grey pattern than as the two others birds (Table 1).

Mean corneal diameter was 8.37 ± 0.17 mm. Visual acuity obtained by the allometric function was 32.55 ± 0.92 c/deg (Table 1).

4. Discussion

Using operant conditioning tests, we estimated the visual acuity in chimango caracaras ranging from 15.08 to 39.83 c/deg. The three individuals tested differed in their visual acuity, particularly one individual showed an extremely low visual acuity compared to the two other birds. This individual took more time to be conditioned and made more errors than the others in the test phase (see Fig. 1 and Table 1). We may have underestimated the visual acuity of this individual because of motivation problems, or this bird may also have a vision defect. Nevertheless, this bird did not behave differently in other situations

Table 1
Information on birds used in the experiment.

Bird	Age (year)	Corneal diameter (mm)	Free feeding weight (g)	Weight in experiment (g)	Weight lost (%)	Number of training session before conditioned	Visual acuity operant conditioning (c/deg)	Visual acuity allometric function (c/deg)
Richard	4	8.2	320	275	14.06	10	39.83	31.62
Kougounia	2	8.2	290	280	3.45	12	30.65	31.62
Flow	2	8.7	285	270	5.26	22	15.07	34.40

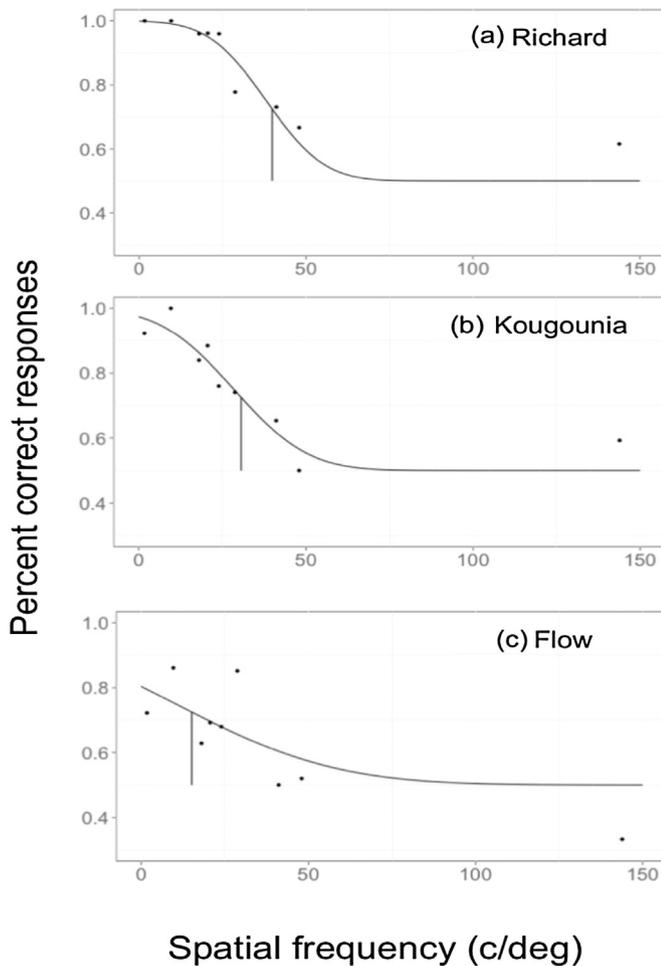


Fig. 1. Psychometric function showing the estimated visual acuity of the three birds. Vertical black bar represents the 0.725 thresholds, defining visual acuity.

such as public demonstration (falconers' observations) and did not show any visual problems. The hypothesis of motivation problem or difficulty for learning task may be the more appropriate. For the two other birds, the visual acuity obtained from operant conditioning (30.65 and 39.83 c/deg) is consistent with allometric estimates (32.55 ± 0.92 c/deg).

We used dark boxes to avoid any sun effect on the screens. We paid attention to this point, and checking the incoming light with a luxmeter inside the boxes. Nevertheless, the light level outside the boxes could change between trials with different whether. It is known that visual acuity depend on luminance [6, 7], and we may have underestimated the visual acuity of our birds. Nevertheless, because the visual acuity estimated by operant conditioning method fit (or overestimated) the visual acuity estimated by allometric function, to our opinion, we can be confident with our method.

Birds of prey are known to have higher resolving power than other birds [1, 16, 19]. Among raptors tested so far, chimango caracara has the lowest visual acuity (lower than the American kestrel *Falco sparverius*: 40 c/deg [10]; Brown falcon *Falco berigora*: 73 c/deg [7], Wedge-tailed eagle *Aquila audax*: 143 c/deg [6] or vultures [11]). This difference could be a result of a lower density of cones in the nasal fovea for the chimango caracara compared to other raptors but also certainly maybe because of a smaller eye (except the American kestrel). Indeed, it seems that the eye size, rather than cones density, could be the main driver to determine the spatial resolution, as showed in passerines [20]. The smaller eye size in the chimango caracara is likely to set the limits of resolution without ruling out the additional possibility that a lower cone density may contribute to the lower spatial acuity. Because

all raptors species where visual acuity has been tested search for preys or carrions mainly from a perch or in flight, they may need higher visual acuity to find their food than the opportunist (in term of diet and foraging) chimango caracara which mainly scans items on the ground [12].

Nevertheless, compared to other, non-raptorial, bird species that have been tested, the chimango caracara has a relatively high visual acuity: e.g. 4 time higher than the opportunist Japanese jungle crows *Corvus macrorhynchos* (8.4 c/deg) [5]. Moreover, the visual acuity of Japanese jungle crows was estimated at near field, and it is known that distance can influence the estimated visual acuity, with higher visual acuity at short distance [21]. It is possible that the relative high visual acuity of chimango caracara compared to the Japanese jungle crow may be a result of its relatedness with falcons [22], that have high visual acuity [7, 10]. Their relatively high visual acuity might also result from the large eye size, as measured by the corneal diameter, since Kiltie [16] found a relationship between eye size and visual acuity. However the chimango caracara has a similar corneal diameter as the domestic pigeon *Columba livia* (6.86 ± 0.42 mm) [23], but more than two times higher visual acuity (3.5 c/deg) [21, 24]. Thus, eye size alone cannot explain the visual acuity difference between these two species. The high visual acuity of the chimango caracara may result from a higher cones and/or ganglion cell density than in the pigeon [19, 23] and a deep fovea that could increase the resolving power [1, 19, 25]. Indeed, all birds of prey investigated so far have a deep central fovea [19]. Unfortunately, to our knowledge, no corneal diameter of Japanese jungle crows was measured or published.

It is known that the size of the visual field differs between bird species according to their different foraging ecology [26, 27], even among raptors [28]. Our study suggests that raptors from different ecology may also differ in their visual acuity: opportunist raptors that forage mainly on the ground may have lower visual acuity than raptors searching prey at long distance. Further comparative studies are needed to explore whether visual acuity differs in raptorial birds in relation to their prey, as found in mammals [13].

Conflict of interest

The authors have no competing interests.

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References

- [1] M.P. Jones, K.E. Pierce, D. Ward, Avian vision: a review of form and function with special consideration to birds of prey, *Journal of Exotic Pet Medicine*. 16 (2007) 69–87.
- [2] D.C. Houston, Scavenging efficiency of Turkey vultures in tropical forest, *Condor* 318–23 (1986).
- [3] G.A. Nevitt, R.R. Veit, P. Kareiva, Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds, *Nature* 376 (1995) 680–682.
- [4] K.O. Donner, The visual acuity of some passerine birds, *Acta zoologica Fennica*. 66 (1951) 1–40.
- [5] K. Yamamoto, I. Furuya, S. Watanabe, Near-field visual acuity in Japanese jungle crows (*Corvus macrorhynchos*), *Physiol. Behav.* 72 (2001) 283–286.
- [6] L. Reymond, Spatial visual acuity of the eagle *Aquila audax*: a behavioural, optical and anatomical investigation, *Vision Res.* 25 (1985) 1477–1491.

- [7] [L. Reymond, Spatial visual acuity of the falcon, *Falco berigora*: a behavioural, optical and anatomical investigation, *Vision Res.* 27 \(1987\) 1859–1874.](#)
- [8] [L. Reymond, J. Wolfe, Behavioural determination of the contrast sensitivity function of the eagle *Aquila audax*, *Vision Res.* 21 \(1981\) 263–271.](#)
- [9] [R. Fox, S.W. Lehmkuhle, D.H. Westendorf, Falcon visual acuity, *Science* 192 \(1976\) 263–265.](#)
- [10] [J. Hirsch, Falcon visual sensitivity to grating contrast, *Nature* 300 \(1982\) 57–58.](#)
- [11] [A.B. Fischer, Laboruntersuchungen und freilandbeobachtungen zum sehvermögen und verhalten von altweltgeiern, *Zool Jahrb Syst.* 96 \(1968\) 81–132.](#)
- [12] [J. Del Hoyo, A.A. Elliot, J. Sargatal \(Eds.\), Handbook of the Birds of the World. Vol. 2. New World Vultures to Guinea-fowl, Lynx Edicions, Barcelona, 1994 1994.](#)
- [13] [C.C. Veilleux, E.C. Kirk, Visual acuity in mammals: effects of eye size and ecology, *Brain Behav. Evol.* 83 \(2014\) 43–53.](#)
- [14] [O. Spiegel, W.M. Getz, R. Nathan, Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? *The American Naturalist.* 181 \(2013\) E102–E115.](#)
- [15] [M. Hall, C. Ross, Eye shape and activity pattern in birds, *J. Zool.* 271 \(2007\) 437–444.](#)
- [16] [R. Kiltie, Scaling of visual acuity with body size in mammals and birds, *Functional Ecology* 14 \(2000\) 226–234.](#)
- [17] [Knoblauch, K. psyphy: functions for analyzing psychophysical data in R. R package version 0.0-5, URL <http://CRAN.R-project.org/package=psyphy>. 2007.](#)
- [18] [H. Wickham, W. Chang, ggplot2: an implementation of the grammar of graphics, *comprehensive R Archive, Network* 2014 \(2014\).](#)
- [19] [O. Inzunza, H. Bravo, R.L. Smith, M. Angel, Topography and morphology of retinal ganglion cells in Falconiforms: a study on predatory and carrion-eating birds, *The Anatomical Record.* 229 \(1991\) 271–277.](#)
- [20] [J.P. Coimbra, S.P. Collin, N.S. Hart, Variations in retinal photoreceptor topography and the organization of the rod-free zone reflect behavioral diversity in Australian passerines, *J. Comp. Neurol.* 523 \(2015\) 1073–1094.](#)
- [21] [S. Bloch, C. Martinoya, Comparing frontal and lateral viewing in the pigeon. I. Tachistoscopic visual acuity as a function of distance, *Behav. Brain Res.* 5 \(1982\) 231–244.](#)
- [22] [C.S. Griffiths, G.F. Barrowclough, J.G. Groth, L. Mertz, Phylogeny of the Falconidae \(Aves\): a comparison of the efficacy of morphological, mitochondrial, and nuclear data, *Mol. Phylogenet. Evol.* 32 \(2004\) 101–109.](#)
- [23] [J. Marshall, J. Mellerio, D. Palmer, A schematic eye for the pigeon, *Vision Res.* 13 \(1973\) 2449–2453.](#)
- [24] [U. Hahmann, O. Güntürkün, The visual acuity for the lateral visual field of the pigeon \(*Columba livia*\), *Vision Res.* 33 \(1993\) 1659–1664.](#)
- [25] [P. Clarke, D. Whitteridge, The projection of the retina, including the 'red area', on to the optic tectum of the pigeon, *Q. J. Exp. Physiol. Cogn. Med. Sci.* 61 \(1976\) 351–358.](#)
- [26] [G.R. Martin, Visual fields and their functions in birds, *Journal of Ornithology.* 148 \(2007\) 547–562.](#)
- [27] [G.R. Martin, What is binocular vision for? A birds' eye view, *J. Vis.* 9 \(2009\) 14.](#)
- [28] [C.T. O'Rourke, M.I. Hall, T. Pitlik, E. Fernández-Juricic, Hawk eyes I: diurnal raptors differ in visual fields and degree of eye movement, *PLoS One* 5 \(2010\), e12802.](#)