Two aberrant serpent-eagles may be visual mimics of bird-eating raptors

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Two independent cases of visual mimicry involving snake-eating eagles as mimics and more powerful bird-eating hawks as models are proposed. One pair of species is formed by the sympatric West African Serpent-eagle *Dryotriorchis spectabilis* and Cassin's Hawk Eagle *Spizaetus africanus* (=*Aquila africana*), inhabiting the tropical forests of the African Gulf of Guinea. The second case involves the Madagascar Serpent-eagle *Eutriorchis astur* and the Madagascar Goshawk *Accipiter henstii*, both sympatric and endemics of forests in Madagascar. Similarity in plumage colour and pattern as well as in body size and proportions are remarkable in both cases. The species mimicry pairs are in both cases not closely related phylogenetically and greatly differ in diet, making it unlikely that common ancestry or shared foraging strategies explain the resemblance in plumage coloration and pattern. Mimicry may have evolved because the mimic serpent-eagles obtain (the following hypotheses are not mutually exclusive): (1) a foraging advantage by deceiving their snake prey as they may not flee from bird-eating raptors such as the models, (2) a lowered predation or harassment by the models or other predators, and/or (3) reduced mobbing by small birds, which tend to avoid bird-eating raptors. Alternatively, the similarities in plumage described here may be the result of random convergence due to constraints in the evolution of plumage colours and patterns in diurnal raptors.

Keywords: bird of prey, mobbing, plumage convergence, plumage pattern, predation, snake eagle

A visual mimic is an organism that has evolved to resemble another species, called the model, with which it does not have a close phylogenetic relationship (e.g. Ward 1976, Edelstam 1985). The best known types of mimicry include: (1) Batesian (or defensive) mimicry, in which a palatable species evolves a resemblance to a powerful or unpalatable species to gain protection against predators; and (b) Müllerian mimicry, defined as the mutual resemblance of multiple, chemically defended prey species. Even if mimicry is agreed upon, to label it as Batesian or Müllerian can be difficult (e.g. Joron & Mallet 1998). Some authors (MacDougall & Dawkins 1998, Edmunds & Golding 1999) have proposed that the criterion used to distinguish between these two main types of mimicry should not only be palatability, but should also include the relative benefit for mimic and

model. If the mimic benefits and the model loses from the resemblance, then the mimicry is Batesian. If both species benefit, this mutualistic relationship is Müllerian mimicry.

Most cases of reported mimicry come from the invertebrate world and include snake-mimicking caterpillars, ant-mimicking spiders, palatable insects resembling distasteful wasps or bees, and innocuous butterflies looking like poisonous ones (Ward 1976). Many bird species are well known as vocal mimics (e.g. Redondo & Arias de Reyna 1988, Hamao & Eda-Fujiwara 2004, Payne *et al.* 2005), but visual mimicry in birds is rare (Diamond 1982, Spear & Ainley 1993) or has gone under-reported, perhaps because alleged mimicry is difficult to prove (Edelstam 1985, Grim 2005) and because DNA-based phylogenetic trees have only become available recently for the main avian groups. This is particularly important because resemblance may be accounted

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for by either close relationship or evolutionary convergence under the constraints of a similar environment and thus bears no relation to mimicry. In addition, and as stated before, mimicry may involve plumage patterns and general appearance, or even egg and nestling mimicry in parasitic birds (Moskát & Honza 2002, Payne *et al.* 2002), but also vocalizations and behaviour (Edelstam 1985), and many bird species have been insufficiently studied in this respect.

Here I propose two independent cases of mimicry involving snake-eating eagles as mimics and bird-eating hawks as models. One pair of species is formed by the sympatric West African Serpent-eagle *Dryotriorchis spectabilis* and Cassin's Hawk Eagle *Spizaetus africanus*, inhabiting the tropical forests of the African Gulf of Guinea. The second case involves the Madagascar Serpent-eagle *Eutriorchis astur* and the Madagascar Goshawk *Accipiter henstii*, both endemics of dense forests on the island of Madagascar. In the latter pair of species the similarity in plumage and shape is so striking that some Madagascar Goshawks in the Bird Collection of the Natural History Museum (Tring, UK) were first labelled as Madagascar Serpent-eagles. I call *Eutriorchis* and *Dryotriorchis* aberrant snake-eagles because they do not conform morphologically to any of the two major types: the *Circaetus*, an African genus with six species, and the *Spilornis*, an Indo-Malayan genus with up to 13 species (Ferguson-Lees & Christie 2001).

METHODS

I examined available skins of the four species involved (i.e. *Eutriorchis astur*, of which only the Type was available, *Accipiter henstii*, *Dryotriorchis spectabilis* and *Spizaetus africanus*) deposited in the Bird Collection of the Natural History Museum (Tring, UK). I also examined all other recognized snake-eating eagles of the world (genera *Circaetus*, *Theratopius*, *Spilornis*, *Polyboroides*, *Harpyhaliaetus* and *Saggitarius*), as well as species of the genera *Spizaetus* and *Accipiter* in the same collection. In the Bird Collection at Estación Biológica de Doñana (Sevilla, Spain), I inspected the only specialist snake-eating falcon, the Laughing-Falcon *Herpethoteres cachinnans*. I also used colour plates, species and diet descriptions, as well as distribution maps in Brown and Amadon (1968) and Ferguson-Lees and Christie (2001).

To compare plumage colours in different body regions (upper-back, breast, tail), reflectance spectra were measured in the range 360–740 nm by using a
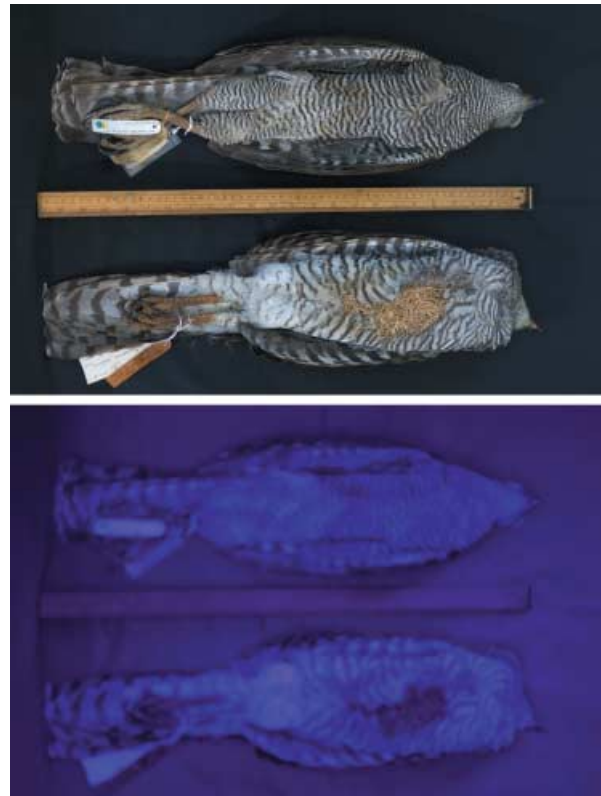

Figure 1. Ventral view of an adult female *Accipiter henstii* (upper), and an unknown sex specimen of *Eutriorchis astur* (lower). Upper, in the visible range, lower in the UV range (30 s exposure).

Minolta CM-2600d portable spectrometer (Minolta Co., Ltd, Osaka, Japan) with UV (xenon flashlight source) and visible light (standard illuminant D65). One specimen per species was also photographed with a digital camera under natural light. To determine whether mimics and models differed in the UV portion of the spectrum, the same specimens were also photographed by mounting a UV filter (B + W UV Black 403 Glass Filter) that does not allow visible light to pass through the lens (Hawlena *et al.* 2006).

RESULTS

The two alleged cases of mimicry are substantiated by the following observations.
(1) The resemblance of colour and pattern of the plumage, along with similar body shape and proportions (Table 1). The similarity between *Eutriorchis*, both in immature and in adult plumage, and the adult plumage of *Accipiter henstii* (Fig. 1), has been stressed by previous authors (Brown & Amadon 1968, Ferguson-Lees & Christie 2001). The similarities are held in the

Table 1. Plumage descriptions, measurements and diet of coexisting raptors: *Eutriorchis astur* and *Accipiter henstii* in Madagascar, *Dryotriorchis spectabilis* and *Spizaetus africanus* in western tropical Africa (based on Brown & Amadon 1968, Ferguson-Lees & Christie 2001).

Eutriorchis astur. Adult. Back brownish slate. Tail same colour with 5–7 blackish bars. Breast and belly white with blackish-brown fine bars. Short and rounded wings with seven longitudinal dark bars. In the mounted specimen I examined, the folded wing reached up to the base of the tail in the body. Very long and rounded tail. Iris, cere and feet yellow. Immature: described as very similar to adult. Slight reversed sexual dimorphism. Wing: 301–341 mm; tail: 274–292 mm; tarsus: 80–92 mm; hallux: 25.3 mm. Diet (one nest): mainly chameleons (genera *Calumna* and *Furcifer*), and geckos (*Uroplatus*); also tree-frogs and snakes.

Accipiter henstii. Adult. Entire upper-parts brownish slate to dark sepia, tail quills with five or six darker bands. Below from chin to undertail coverts white barred closely with dark brown or black. Short and rounded wings streaked with longitudinal dark bars. Eye, cere and feet yellow. Immature: above brown, with feathers edged rufous. Below rufous buff, with large drop-shaped or oval dark brown streaks and spots. Marked reversed sexual dimorphism, as in other *Accipiter* spp. Wing: 276–283 mm (male), 318–330 mm (female); tail: 244–258 mm (m), 288 mm (f); tarsus: 81–85 mm (m), 95–100 mm (f); hallux: 33.85 mm. Diet: forest birds, some mammals (lemurs) and poultry at farms.

Dryotriorchis spectabilis. Adult. Medium-sized hawks. Wings short and rounded. Tail very long and rounded. Feathers of top of head slightly pointed, forming a suggestion of a crest. Upper-parts dark brown. Cheeks light brown, throat ferruginous, a black malar streak and a black streak down centre of throat. Under-parts white, with large round blackish spots surrounded by a ferruginous wash (*D. s. spectabilis*). Centre of the under-parts plain white, spots confined to the flank (*D. s. batesi*). Eyes dark brown or grey, cere, legs and feet yellow. Immature: crown and mantle basally white. Under-parts closely spotted with round ferruginous and blackish spots. Slight reversed sexual size dimorphism. Length: 54–60 cm; wing-span: 94–106 cm. Wing-chord: 295–315 mm; tail: 245–268 mm; tarsus: 66–70 mm; hallux: 27.4 mm. Diet: snakes, lizards, chameleons, amphibians.

Spizaetus africanus. Adult. It appears as a small eagle, with short rounded wings and a long rounded tail. Dark above and almost all white below. Legs feathered. Eye pale yellow to brownish yellow, cere and feet yellow. Immature: head cinnamon rufous, dusky on lores, streaked on throat and centre of crown with black. Breast russet with half-concealed blackish spots, paler and more heavily spotted on flanks and abdomen. The immature changes to the adult by growing blacker above and whiter below. Strong reversed sexual size dimorphism. Length: 50–56 cm; wing-span: 103–113 cm. Wing-chord: 330–341 mm (m); tail 211–234 mm; tarsus 70–84 mm; hallux: 34–36 mm. Diet: forest birds and tree squirrels.

UV range, with no hidden patterns emerging in this portion of the spectrum if models and mimics are photographed side by side with a UV filter (Fig. 1). In fact, UV reflectance is low compared with the visible region, at least in the portion of the spectrum recorded by the spectrometer (see Figs 4 & 5). That *Eutriorchis* is the mimic and *A. henstii* the model is given by that fact that *A. henstii* resembles goshawks of the genus *Accipiter*, looking very much like the Northern Goshawk *A. gentilis* of Eurasia and North America (Brown & Amadon 1968). *Eutriorchis*, however, has been considered *incerta sedis*, traditionally classified among the snake-eating eagles due to anatomical traits other than plumage, including legs and toes with polygonal scutella (the taxonomy of raptors has relied heavily on beak and foot structure, Feduccia 1999).

The similarities between *Dryotriorchis* and *Spizaetus africanus* are less obvious than in the preceding case, but Brown and Amadon (1968) recognized that '*Dryotriorchis* could possibly be confused with *Spizaetus africanus*', and described both species as short-winged eagles with a long rounded tail. There are two recognized subspecies of *Dryotriorchis*. The adult form of *D. s. spectabilis* resembles more closely the immature plumage of *S. africanus* (Fig. 2), whereas *D. s. batesi* resembles the adult plumage of *S. africanus* (Table 1, Fig. 3). As in the preceding case, the plumage similarities are also kept in the UV range, both using UV photography (Figs 2 & 3) and when comparing reflectance spectra (Fig. 5).

Again, I believe *Dryotriorchis* is the mimic and *Spizaetus* the model because the latter is a recognizable eagle with feathered tarsi, as are all other species in the subfamily Aquilinae (Lerner & Mindell 2005), whereas *Dryotriorchis* is a unique, small serpent-eagle unlike any other. It is much smaller than the remaining species of African snake-eagles in the genus *Circaetus*, and has different proportions (Brown & Amadon 1968). In addition, it bears no resemblance to any of the species in the other major group of serpent-eagles, the Indo-Malayan *Spilornis*. The fact that *Dryotriorchis* is in a monotypic genus also indicates that the taxonomists who named the species found enough morphological differences with other snake-eating eagles to warrant separate status. By contrast, the distinctiveness of *S. africanus* compared with its relatives within the subfamily Aquilinae has never been considered large enough to place this species in a separate genus. Nonetheless, it has to be noted

Figure 2. Ventral view of *Dryotriorchis s. spectabilis*, adult from Liberia (above) and *Spizaetus africanus*, an immature from Sierra Leone (below). Upper, in the visible range, lower in the UV range (30 s exposure).

Figure 3. Ventral view of *Dryotriorchis s. batesi*, adult from Cameroon (below) and *Spizaetus africanus*, an adult from Liberia (above). Upper, in the visible range, lower in the UV range (30 s exposure).

that *Spizaetus* has recently been discovered to be polyphyletic (Helbig *et al.* 2005, Lerner & Mindell 2005), with *S. africanus* clustering with species of the genera *Aquila* and *Hieraaetus*, being more distantly related to the remaining *Spizaetus*. It should be named *Aquila africana* (following Sangster *et al.* 2005) and thus would still belong in the subfamily Aquilinae.

(2) The sympatric distribution of each pair of species. Mimicry is only capable of evolving if the species share the same habitat. Both pairs of species coexist in dense forests, either in the Gulf of Guinea or in coastal Madagascar (see Ferguson-Lees & Christie 2001 for distribution maps).

(3) The distant phylogenetic relationship between members of each pair of species precludes that similarity emerged due to common ancestry. *Eutriorchis* was originally classified as an aberrant snake-eating eagle that Brown and Amadon (1968) suggested could be united with *Dryotriorchis*. However, it has recently been established that *Eutriorchis* is related to the Bearded

Gypaetus barbatus, Egyptian *Neophron percnopterus* and Palm-nut *Gypohierax angolensis* Vultures of the subfamily Gypaetinae (Lerner & Mindell 2005). *Eutriorchis* could therefore be described as a vulture that looks like a goshawk in a clade where all the other species are also peculiar in their feeding habits and behaviour: either eating bones after breaking them against rocks and using cosmetics (Bearded Vulture, Negro *et al.* 1999), breaking ostrich eggs with stones as well as eating cow dung (Egyptian Vulture, Negro *et al.* 2002) or eating palm nuts (Palm-nut Vulture, Mundy *et al.* 1992). The model of *Eutriorchis*, *A. henstii*, has not been analysed molecularly, but other members of the subfamily Accipitrinae, *A. bicolor* and *A. cooperii*, have been placed far away from *Eutriorchis* and the Gypaetinae, in a clade along with the harriers *Circus* spp. (Lerner & Mindell 2005).

Dryotriorchis, by contrast, and with high support in the molecular phylogeny proposed by Lerner and Mindell (2005), falls within the clade of typical African snake-eating eagles of the genus *Circaetus*. It
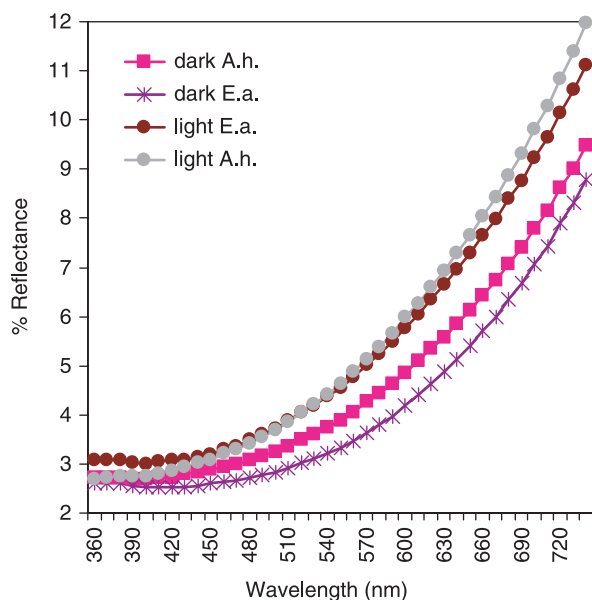
Figure 4. Spectral reflectance curves of the dark and lighter colour bands in the central tail feather (upper side) of specimens in Figure 1, *E. astur* (E.a.) and *A. henstii* (A.h.), obtained with a Minolta CM-2600d spectrometer. The two upper curves, almost overlapping, correspond to the lighter brown colour in the tail. The two lower curves correspond to the darker terminal bands.

Figure 5. Spectral reflectance curves (from top to bottom) of the whitish breast of *S. africanus* (S.a.) and *D. spectabilis* (D.s.) in Figure 3, throat region of *E. astur* (E.a.) and *A. henstii* (A.h.) in Figure 1, back of *E. astur* and *A. henstii* in Figure 1. All curves were obtained with the use of a Minolta CM-2600d spectrometer.

is thus a genuine serpent-eagle by descent (Circaetinae subfamily) and by food habits. Even if included in the genus *Aquila*, *S. africanus* has always been placed in the subfamily Aquilinae using either morphological or DNA-based evidence.

(4) The mimics are outnumbered by the model (see population figures in Ferguson-Lees & Christie 2001), particularly in the case of the Madagascar Serpent-eagle, which was thought to be extinct for over 50 years. Evolutionary theory predicts that the advantage of being a mimic will increase as the model becomes relatively more common (Owen 1980). Nonetheless, highly deterrent models, such as the heavily armed *S. africanus* or *A. henstii*, need not occur at a higher density to be beneficial to the mimic (Edelstam 1985).

(5) The dietary difference within each pair of species (a bird-eater versus a snake-eater, Table 1) suggests that morphological resemblance is not the result of evolutionary convergence due to shared foraging behaviour or food habits. Resemblance ends in the structure and size of the feet, in accordance with the known diets of the bearers. Bird-eating *A. henstii* and *S. africanus* have longer and more powerful claws than the snake-eating *E. astur* and *D. spectabilis* (see hallux length in Table 1).
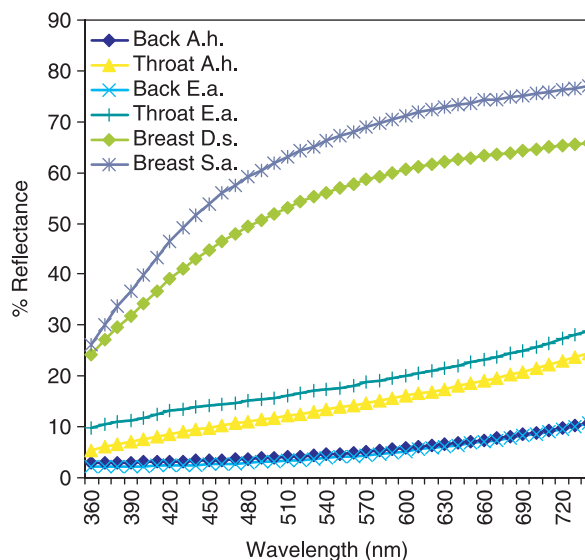
DISCUSSION

There are few reported cases of visual mimicry in Aves. The best known examples (Bortolotti 2006) include Cuckoos *Cuculus canorus* resembling *Accipiter* hawks to induce mobbing so that they can locate potential hosts (del Hoyo *et al.* 1997), a group of several Melanesian orioles *Oriolus* spp. mimicking pugnacious honeyeaters *Philemon* spp. to reduce interspecific aggression (Diamond 1982), and Kermadec Petrels *Pterodroma neglecta* that may take advantage of their resemblance to skuas (subfamily Stercorariinae) to parasitize other seabirds, thus being aggressive or foraging mimics (Spear & Ainley 1993). More recently, a case of Müllerian mimicry in the only known group of birds with toxic plumages, the pitohuis *Pitohui* spp., has been reported (Dumbacher & Fleischer 2001). That visual mimicry in birds warrants a systematic search is demonstrated by the fact that new cases are still emerging (e.g. Witt 2005).

The two cases of visual mimicry that I have presented here are unusual in the sense that they involve predators instead of prey. It can be argued that the species involved may still be killed or harassed by larger or more powerful predators, but alternative explanations to predation-avoidance are also possible for the evolution of these mimicry pairs, as with the few previously reported cases involving other birds

of prey. Willis (1976) suggested that the insectivorous Rufous-thighed Kite *Harpagus diodon* was mimicking the bird-eating Bicolored Hawk *Accipiter bicolor*, and that the kite was taking advantage by scaring off birds that could disturb its prey. The false faces of predatory birds, mostly falcons, may mimic owl faces to provoke mobbing and get closer to prey (Negro *et al.* 2007). An interesting case of aggressive mimicry involves the paradoxical white morph of the Grey Goshawk *Accipiter novaehollandiae* that may have evolved in response to the presence of White Cockatoos *Cacatua galerita* (Edelstam 1985). Cockatoos are innocuous to other birds and a cockatoo-mimicking goshawk might thus approach its prey unnoticed. The remaining cases of mimicry in raptors reported to date are the honey buzzards *Pernis* spp. mimicking pugnacious *Spizaetus* eagles, and the Zone-tailed Hawk *Buteo albonotatus* mimicking the Turkey Vulture *Cathartes aura* (Edelstam 2001).

Possible explanations of mimicry in snake-eagles

First, *Eutriorchis* and *Dryotriorchis* may be mimicking specialist bird-eating raptors to deceive their snake prey and make them believe they will not be attacked (hypothesis suggested by K. Omland). This idea has been proposed for the Zone-tailed Hawk mimicking non-predatorial Turkey Vultures (Edelstam 2001, see above) and cannot be discarded. That a predator–prey relationship may play a role in the evolution of plumage morphs in raptors has already been suggested, although specifically for mammal hunters (Roulin & Wink 2004). For this hypothesis to work in our mimicry pairs, the snake species involved should have very good vision and the ability to distinguish between differently coloured predators. It has already been suggested that for many snakes vision may be important in predator detection (Bonnet *et al.* 1999), but visual acuity possibly varies enormously among species (R. Shine pers. comm.).

Secondly, the mimics may benefit from lower predation or harassment from the models themselves (which may be less prone to attack conspecifics) or by predators that would not dare to confront either *S. africanus* or *A. henstii*, both with more formidable talons than their mimics (see Table 1). *Dryotriorchis* and *S. africanus* coexist in dense tropical forests with the much larger and heavily armed Crowned Hawk Eagle *Stephanoetus coronatus* capable of killing small antelopes, monkeys and forest birds (Ferguson-Lees & Christie 2001). Unfortunately, there are no records

of interactions between any of these three raptor species. In Madagascar there is no larger forest hawk than *A. henstii* that can possibly be considered the top avian predator there. The lack of large avian predators, carnivores and venomous snakes in Madagascar weakens the predation-avoidance hypothesis for the origin of the mimicry of *E. astur* on *A. henstii*, unless the former is trying to avoid attacks by the latter.

A third hypothesis for the origin of these mimicry cases would be reduced mobbing by birds, an explanation also advanced for the case of *Buteo albonotatus* mimicking the innocuous *Cathartes aura* (Willis 1963, Edelstam 1985), which seems to be ignored by passerines. In the case of the bird-eating raptors, however, they may be mobbed at reduced rate relative to other raptor species because of the higher risk passerines would incur (although this is only an assumption as no studies have been made). Mobbing, especially by passerine birds, has recently been identified as an important selective force in the plumage evolution of birds of prey and owls (Negro *et al.* 2007). Mobbing is a constant nuisance for numerous raptorial birds, including large and well-armed birds such as *Aquila* species (J.J. Negro pers. obs. on Imperial *Aquila heliaca* and Golden *Aquila chrysaetos* Eagles). Mobbing may interfere with hunting or social activities of raptors, and there is even the case of a population of Pygmy Owl (*Glaucidium passerinum*) that may have been mobbed to extinction in the Black Forest of Germany (Mikkola 1983). Last but not least, mobbing seems to be a partially innate response that does not require a perfect raptor model (Hinde 1954a, 1954b), and we have even elicited mobbing responses (J.J. Negro pers. obs.) by different passerine species using a plastic cast of a Hobby *Falco subbuteo* in both Spain, where the Hobby is a native species, and Argentina, where it is not (Ferguson-Lees & Christie 2001).

An alternative hypothesis to explain the resemblance within each pair of species would be random convergence, due to constraints in colour and/or pattern production. The convergence of complex plumage patterns with no obvious adaptive explanations has been reported in orioles *Icterus* spp. (Omland & Lanyon 2000, Omland & Hofmann 2006) and other avian taxa (Price & Pavelka 1996). It may be argued that the plumage of raptors might conform to a limited pattern, where feather colour is due to melanin (i.e. brown, grey or black hues) and/or its absence (i.e. white coloration). Nonetheless, raptor plumages still vary immensely, with practically white species and almost black ones. In addition, shapes

and sizes also vary enormously. I thus believe that the striking similarities in colour, plumage pattern and body size in the cases reported here are better explained by the existence of mimicry mediated by one or a combination of the above-mentioned hypotheses.

Therefore, assuming that the cases reported here are true instances of visual mimicry, the next question is to categorize it as Müllerian or Batesian in terms of benefits or losses for the models. If the presence of the mimics, with which there is little or no dietary competition, helped to reduce the presence of true competitors, such as smaller species of the genus *Accipiter* co-occurring in both the tropical forest of Western Africa (i.e. *A. tachiro, A. castanilius, A. badius, A. erythropus*) and Madagascar (*A. madagascariensis, A. francesii*), then the interaction could be considered mutualistic, and we could define it as Müllerian mimicry (MacDougall & Dawkins 1998). Alternatively, if potential prey were scared off by the mimic, the model would lose hunting opportunities and the relationship would be parasitic. Thus, it could possibly be described as Batesian mimicry. Models and mimics in this study are possibly very hard to investigate in the wild due to their own rarity and the rough habitat they live in. However, if field observations were ever undertaken, it would be useful to record any possible behavioural interactions between models and mimics, mimics and their snake prey, as well as between both models and mimics and potentially mobbing birds. In addition, and specifically to test the first hypothesis mentioned above, the visual acuity of the snake species preyed on by *Eutriorchis* and *Dryotriorchis* should be determined. These observations may help to elucidate whether the adaptive hypotheses exposed above are plausible or not.

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