Biological Journal of the Linnean Society, 2007, **90**, 467–477. With 3 figures

Deceptive plumage signals in birds: manipulation of predators or prey?

JUAN JOSÉ NEGRO[1], GARY R. BORTOLOTTI[2]* and JOSÉ HERNÁN SARASOLA[1]

[1]*Department of Applied Biology, Estación Biológica de Doñana, Avda de María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain*
[2]*Department of Biology, University of Saskatchewan, 112 Science Pl, Saskatoon SK S7N 5E2, Canada*

Received 11 October 2005; accepted for publication 1 May 2006

Several species of raptors have two ocelli (eye-like patches) in the back of their head, giving them the appearance of a false face, although this trait has rarely been reported. According to our observations, these markings may be widespread in the family Falconidae, some *Accipiter* hawks, and some owls (e.g. *Glaucidium*, and some *Athene*, *Aegolius*, and *Surnia*). In this study, we outline general classes of hypotheses that may account for ocelli on the heads of raptors. The most frequently evoked general hypothesis is that ocelli offer protection against attackers. For example, a predator may abort the effort, be deflected by the ocelli, or be warned that the bearer will retaliate if attacked. We propose two alternatives. Most raptors with ocelli typically include a large proportion of passerine birds in their diets. The false faces may have evolved to aid in the hunting of small birds by actually provoking, or manipulating the nature of, a mobbing response. The benefit of doing so may either be immediate because there are numerous accounts of mobbers being killed, or the benefit may be postponed if the predator is using mobbing as a means of evaluating hunting prospects in a given area. An analysis of the pygmy-owls of the genus *Glaucidium* indicates that species displaying ocelli in the nape tend to have a high proportion of small birds in their diets and live in open habitats, whereas the opposite is true for species without ocelli. Pygmy-owls with ocelli are also considerably smaller and, collectively, these findings are most consistent with false faces being a conspicuous visual signal to deceive mobbing birds so they can be preyed upon. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **90**, 467–477.

ADDITIONAL KEYWORDS: deceptive signal – false face – hunting techniques – mobbing – ocelli – raptors.

INTRODUCTION

The coloration of animals may be adaptive in at least three different ways: (1) providing camouflage; (2) for communication in intra- or interspecific interactions; and (3) serving a physiological function (e.g. protecting against ultraviolet radiation) (Burtt, 1981; Savalli, 1995; Ortolani, 1999). As an example of case 2, animals of widely different taxa, including vertebrates and invertebrates, are said to deceive predators by displaying conspicuous colour markings in parts of their bodies; but see also Zahavi & Zahavi (1997). Perhaps some of the best known examples involve ocelli, or 'false eyes', on the wings of moths or on the bodies of some caterpillars and fish (Cott, 1940).

In this study, we are concerned with the 'false face' exhibited on the back of the heads of birds of prey, both diurnal raptors and owls. These markings have passed unnoticed or at least unreported so far for most species, except for the American kestrel (*Falco sparverius* L.) (Clay, 1953), pygmy-owls of the genus *Glaucidium* (Steyn, 1979; del Hoyo, Elliot & Sargatal, 1999; Deppe *et al.*, 2003), and, more recently, the Eurasian hobby (*Falco subbuteo* L.) (Negro, Grande & Sarasola, 2004). The effect of a 'false face' is generally achieved by the presence of two rounded spots in the occipital area, which are either lighter or darker in colour than the surrounding plumage in the head. These markings have also been termed occipital spots, nuchal or nape patches, eyespots, false eyes, dorsal faces, and combinations of related terms. We use ocelli for the spots and false faces for the overall visual phenomenon, but

*Corresponding author. E-mail: gary.bortolotti@usask.ca

emphasize that this should not bias the interpretation of function. However, in birds at large, ocelli are also found in nonraptorial species such as the peacock (*Pavo cristatus* L.), wild turkey (*Meleagris gallopavo* L.), and some pheasants (del Hoyo, Elliot & Sargatal, 1994). These ocelli are rounded spots formed by circular patterns and colours and often are more eye-like in appearance in that they typically have a pupil. They tend to occur in single feathers, although an individual bird can display many of them as in the peacock's train. These single-feather ocelli appear to play a role in mate choice (Petrie, Halliday & Sanders, 1991). Due to their developmental complexity, these ocelli appear to be costly traits, and probably evolved through sexual selection (Andersson, 1994; Maynard Smith & Harper, 2003).

The ocelli on the heads of raptors (here including both hawks and owls) are of a different nature than those of peacocks and pheasants. The former are a visual effect created by several small, similarly coloured contour feathers on the nape, which visually stand out against contiguous contour feathers of a different colour (for a description of ocelli in hobbies, see Negro *et al*., 2004). Unlike the ornamental, single-feather ocelli that are found exclusively on males, ocelli of birds of prey do not meet the criteria for sexually selected traits (Andersson, 1994) because, within species, they often occur in both sexes and all age groups including nestlings. Although the most common explanation for ocelli is that they confer protection against predators (Cott, 1940), there is no single test of this hypothesis for birds.

The possible functions of the ocelli of the American kestrel and pygmy-owls have been debated. Clay (1953) proposed that the evolution of such a complex pattern in the American kestrel by chance alone was highly improbable, and suggested plausible functions: (1) the ocelli were 'deflective' marks, *sensu* Cott (1940), to misdirect the attack of predators or mobbing birds and (2) prey, in particular small birds, might be mislead as to where an attacking kestrel was actually looking (although he did not give much credence to this idea). Mueller (1971) proposed that the ocelli of the American kestrel were used in territorial contests although this appears to unlikely given what is known of this species' behaviour (Balgooyen, 1975). The ocelli of kestrels may instead give the illusion of watchful eyes that would make predators or competitors think that the falcon had discovered them (Balgooyen, 1975). More recently, Deppe *et al*. (2003) used painted wooden models of northern pygmy-owls (*Glaucidium gnoma* Wagler) with and without occipital ocelli to test whether avian mobbers were influenced, or not, by those markings. The presence of ocelli appeared to redirect the attacks towards the front of the model, and thus the study by Deppe *et al*. (2003) provides the first empirical evidence for a link between ocelli and avian mobbers.

The American kestrel and the pygmy-owls are not unique among birds of prey in having ocelli. The recognition of several new species with such plumage traits warrants a quest for general explanations. In our opinion, there are two general classes of hypotheses: (1) the illusion of false faces may confer protection to the bearers or (2) they may be an aid in capturing prey. Here, we present a description of the phenomenon in several raptors where it has been previously unreported. We also review mobbing behaviour because it provides a crucial perspective for several arguments, and propose a series of functional hypotheses for the evolution of raptorial ocelli. We outline predictions of these hypotheses and test them using the genus *Glaucidium*, a large group of owls characterized for having evolved the most perfect and undisputed nuchal ocelli/false face in birds (at least to human eyes).

SPECIES WITH OCELLI

We have only found published references to a 'false face' in American kestrels, pygmy-owls, the northern hawk owl *Surnia ulula* L. (del Hoyo *et al*., 1999; Svensson *et al*., 2000), the Eurasian hobby (Negro *et al*., 2004), and two little owl species of the genus *Athene* (König, Weick & Becking, 1999). In addition, Jenkins, Wagner & Hoffman (1991) mentioned 'nape patches' for the Taita falcon (*Falco fasciinucha* Reichenow and Neumann), and Steyn (1979) describes ocelli in the bat hawk (*Macheiramphus alcinus* Bonaparte). Our sources for determining the presence of ocelli in raptors have been, in part, colour plates and photographs in books, including field guides and handbooks (Cramp & Simmons, 1977; del Hoyo *et al*., 1994, 1999; Forsman, 1999; König *et al*., 1999; Svensson *et al*., 2000; Wheeler, 2003). A general problem with bird plates and photos is that individuals tend to be presented frontally. In addition, artists may sometimes misrepresent the markings, and species descriptions do not usually include the back of the head. Therefore, we also examined museum specimens, and live birds in the field, zoos, rehabilitation centres, and private collections (see Acknowledgements).

The family Falconidae shows a high prevalence of species with ocelli, and it is clear that these markings have appeared in phylogenetically distinct lineages (Fig. 1). It is not our intention to present an exhaustive survey and a description of species. A more complete analysis within *Falco* will be presented elsewhere (G. R. Bortolotti and J. J. Negro, unpubl. data). We have chosen examples where ocelli/false faces are reasonably distinct and usually present in males and females of both young and adults (Fig. 1).

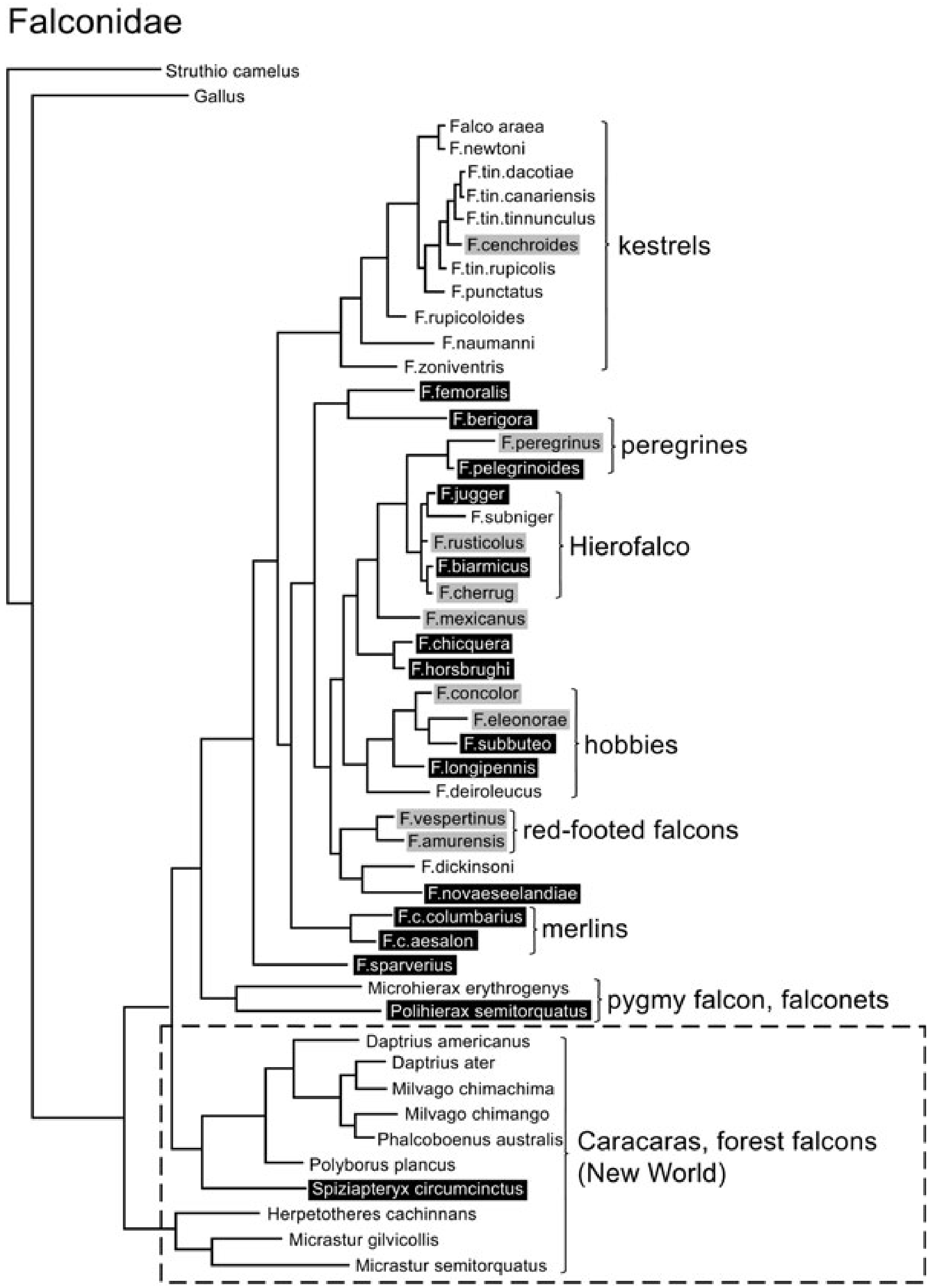

Figure 1. Phylogenetic tree of the Falconidae based on the sequence of the mitochondrial cytochrome *b* gene, adapted from Wink & Sauer-Gürth (2004). The black highlighted taxa are species for which ocelli are present. The grey highlighted taxa have ocelli in only some plumages (e.g. depending on sex and age). The remaining taxa do not have ocelli.

In some species, such as the peregrine falcon (*Falco peregrinus* Tunstall), the presence of ocelli is age- and subspecies-dependant. Even within the species presented, the markings of interest are not always obvious and may require a particular perspective or feather disposition of the birds under observation. The ocelli of some species are hardly visible when the feathers are flattened over the head, as in museum specimens (Clay, 1953), which may explain why these spots have been overlooked or misrepresented in most species. Ocelli as discussed here are located on the nape and in two visually distinct areas. In the Falconidae, the occipital spots are round or elliptical and of a lighter colour than the surrounding feathers. However, in American kestrels, and lanner (*Falco biarmicus* Temminck) and barbary (*Falco pelegrinoides* Temminck) falcons, ocelli are dark patches surrounded by a lighter colour. In the latter species, the ocelli may mimic the true eyes of the bird in the front. However, in species where the ocelli are light in colour, they may cover much of the back of the head when fully displayed and convey the impression of an owl's facial disk. In this case, of which hobbies and saker falcons (*Falco cherrug* Gray) are good examples, it may be more appropriate to speak of a 'false owl face'. The image of a face per se is reinforced in many species by the appearance of the triangular dark stripe pointing down that separates the two spots, and may mimic a raptor's bill (Balgooyen, 1975).

The owl illusion is reinforced in falcons because they have rather short necks and blunt faces (Cade, 1982; del Hoyo *et al*., 1994). They are also big-headed to accommodate their large eyes, more so when they fluff out the feathers of the cheeks, nape, and crown (Cade, 1982), when the ocelli are typically most visible. Because the ocelli are located side by side, an owl-like image is particularly evident because Strigiformes are the only birds with frontally placed eyes. Falcons are thus morphologically preadapted to resemble owls. Furthermore, Clay (1953) noticed that the American kestrel's habit of head-bobbing accentuated the conspicuousness of the ocelli and enhanced the resemblance of the ocelli to the eyes of an owl.

In the case of the Falconidae, the spots are distinct areas separated by entire feathers of a different colour. By contrast, many Accipitridae have a single pale area on the back of the head previously described as the cryptic occipital spot by Hafner & Hafner (1977). For most hawks and allies, this large, triangular area of basally white feathers gives a very different visual effect than the occelli we discuss here. However, both sparrowhawks (*Accipiter nisus* L.) and bat hawks (Steyn, 1979) show two distinct spots even though the pale coloration (at the base of black-tipped feathers) is not confined to two areas of the head (G. R. Bortolotti, J. J. Negro & J. H. Sarasola, pers. observ.).

In the case of pygmy-owls, ocelli are typically distinct spots, as they are in the Falconidae, which are dark (black or brown) and resemble enlarged true eyes. Approximately three-quarters of the many species of pygmy-owls (depending on the taxonomy used) have such spots (König *et al*., 1999; see below). In some cases (e.g. *Glaucidium tephronotum* Sharpe) spots are indistinct whereas, in others, they may appear but be incorrectly identified as a nuchal collar (Finch-Davies & Kemp, 1980: 330). For those species with ocelli, the owls seem to mimic themselves with remarkable accuracy (Bent, 1961; Steyn, 1979). The effect of a false face is reinforced in some species of *Glaucidium* and *Athene* by the presence of whitish eyebrows over the dark, rounded spot (König *et al*., 1999). Ocelli in *Athene* tend to not be as distinct as in pygmy-owls and are apparently lacking in some populations (e.g. *Athene noctua* Scopoli) (G. R. Bortolotti & J. J. Negro, pers. observ.), nor are they immediately obvious in *Surnia*, where a false face is created by diagonal stripes running from the top of the head to the nape (Svensson *et al*., 2000; Johnsgard, 2002; G. R. Bortolotti & J. J. Negro pers. observ.). Johnsgard (2002) suggested that these diagonal stripes might be an evolutionary precursor to the ocelli of pygmy-owls. We have also observed these diagonal stripes and false faces on the saw-whet (*Aegolius acadicus* Gmelis) and boreal (Tengmalm's) (*Aegolius funereus* L.) owl.

AVIAN MOBBING

Mobbing is a widespread antipredator behaviour in animals (Ostreiher, 2003) that is commonly employed by passerine birds against diurnal raptors and owls (Curio, 1978a, b; Caro, 1986). A considerable amount of research has been conducted on both proximate factors that elicit mobbing (Hinde, 1954a, b; Altmann, 1956; Curio, 1975), and its potential adaptive significance (Curio, 1978a, b; McLean & Rhodes, 1991). The question of the adaptive significance of avian mobbing is far from being solved (McLean & Rhodes, 1991; Zahavi & Zahavi, 1997). The reason why so much effort has been put into studying the harassment of predators involves the great risks posed by such behaviour, and the nature of the consequences to predators. It is clear that, in many cases, mobbing birds place themselves in deadly risk by approaching their predators (Curio & Regelmann, 1985; Sordahl, 1990). During mobbing, individuals come close to their potential predators and move around them emitting alarm calls (Altmann, 1956). The literature abounds with examples where mobbers actually strike their targets, and it is not uncommon for them to be so absorbed in the attacks that they continue the behaviour long after the predator has left the area (Altmann, 1956; Sparks & Soper, 1989; G. R. Bortolotti, J. J. Negro & J. H. Sarasola, pers. observ.). Mobbers may even be at risk from secondary predators because they can be so fixated on their target (Altmann, 1956; Walker, 1983). Humans have exploited this behaviour by attracting birds for the purpose of killing them for food by using owls as lures (Sparks & Soper, 1989). There are also numerous reports of harassers being killed by the predator they are mobbing (Curio & Regelmann, 1985; Poiani & Yorke, 1989; Sordahl, 1990; J. L. Alcaide pers. comm.). Although the costs seem obvious, the specific benefits of mobbing are far from clear (McLean & Rhodes, 1991; Ostreiher, 2003). Harassment may force raptors to 'move on' to other areas (Flasskamp, 1994), or provide a way to increase social status or 'prestige' to the mobbers (Zahavi & Zahavi, 1997).

It is clear that mobbing behaviour can negatively affect raptors in a variety of ways. The damage may vary from lost hunting opportunities (Bildstein, 1982; Flasskamp, 1994; Pavey & Smyth, 1998), to suffering distress and physical damage (Poiani & Yorke, 1989; Koehler, 1992; Flasskamp, 1994), or death (Bent, 1961), and there may even be population consequences because it has been suggested (Mikkola, 1983: 116) that the Eurasian pygmy-owl (*Glaucidium passerinum* L.) in the Black Forest of Germany was mobbed to local extinction.

HYPOTHESES FOR THE FUNCTION OF FALSE FACES IN PREDATORS

Unlike other predator–prey relationships that may have given rise to defensive false faces in prey species, such as in moths hunted by birds, here we have a signalling predator with three potential types of receivers: (1) predators; (2) prey of the signaller; (3) and conspecifics. A deceptive false face may protect its bearer against surprise attacks by any of the three types of receivers. However, if the signal was an aid in hunting, it would only be directed to the behaviour of potential prey. Along with formulating the hypotheses, we briefly present predictions regarding both the signal (i.e. its detectability) and the signaller (i.e. attributes of the raptor) (Table 1).

PROTECTION HYPOTHESES

Preconditions for the following group of hypotheses are that the species involved, even though they are predators themselves, are in turn depredated or are at risk in intraspecific conflicts, or are harassed by other animals (i.e. mobbers).

Hypothesis 1: deceptive detection

Deceptive detection refers to the fact that a predator may be fooled into thinking that the prey (the raptor in this case) is actually aware of the predator when it is not. Descriptions of how this would work have so far focused on the false face functioning to abort a strike (Clay, 1953). However, we believe a more plausible scenario is that the ocelli would give the appearance that the raptor (as prey) was vigilant, and hence an attack by another raptor would not be initiated. Hafner & Hafner (1977) suggested that the cryptic occipital spot of the Accipitridae could function in deflection. They proposed that the bright white spot formed a 'facial disc' that would deflect predatory attacks on sleeping birds. We believe this is implausible because the single spot does not appear face-like and, as noted by Hafner & Hafner (1977), it makes the individual more conspicuous, which surely must be disadvantageous to a roosting bird. Steyn (1979) proposed that the false face may be advantageous when a pygmy-owl was on its nest and a predator, upon inspecting the cavity, would see a hint of a face in the darkness.

Hypothesis 2: deflection to less vital parts of the body

This hypothesis assumes that the attackers, whether predators, conspecifics or mobbers, aim at the eyes of their victim, which are the most sensitive areas in the head. Contrary to the previous hypothesis, the attack actually takes place, but as the attacker is fooled, blows are directed to the back of the head. This deflection hypothesis has been well developed by Cott (1940)

Table 1. Summary of predictions for five hypotheses under two general categories, protection or predatory aid, concerning the function of ocelli in raptors

	Protection			Predatory aid	
	Deceptive detection	Deflection	Startle	Mobber manipulation	Mobber census
Detectability of the signal					
Permanent ocelli	Y	Y	N	Y	Y
Ocelli displayed at will	N	Y	Y	Y	Y
Open habitat	Y	–	–	Y	Y
Attributes of the raptor					
Conspicuous behaviour	N	N	N	Y	Y
Birds in diet	–	–	–	Y	Y
Agile	–	–	–	Y	–

Y = yes for supportive; N = no for incongruent; – = no directional prediction.

for many taxa. Bold elements of coloration, such as ocelli, are target-like and deflect enemies from more to less vital parts of the body. When watching mobbing birds, it is clear that dives are preferentially directed at the heads of predators (G. R. Bortolotti, J. J. Negro & J. H. Sarasola, pers. observ.). However, at least for owls with no ocelli (e.g. *Bubo virginianus*) passerines attack the back of the head, which should be less vulnerable than the front (Heinrich, 1987). That false eyes can change the directionality of attacks by mobbers has been demonstrated experimentally by Deppe *et al*. (2003). Models of pygmy-owls without ocelli were attacked from the rear; however, when eyespots were painted on the back of the head, passerines redirected attacks to the front. These observations suggest that the deflection hypothesis, although having intuitive appeal, is unlikely.

Hypothesis 3: startle response

This hypothesis has not been typically evoked for birds (but see Deppe *et al*., 2003), but has been proposed for conspicuously patterned wings on moths (Schlenoff, 1985). The sudden display of a contrasting colour pattern in the head may have an effect on attackers by inducing a 'startle' response. This is especially plausible for the many species with ocelli that are largely visible only after ptiloerection, which is the normal response of an individual in a heightened state of alert. Shown to a predator, the ocelli would give prey a chance to escape. Shown to mobbers, they may induce a fear response to prevent close approach or to make attacks less accurate. Against aggressive conspecifics, the sudden display of contrasting colour could give a potential victim time to escape or retaliate.

Hypothesis 4: aposematic signal

It has recently being proposed (Newman, Buesching & Wolff, 2005) that dark facial masks of medium-sized mammalian carnivores are aposematic (i.e. warning of aggressive defensive behaviour that could be harmful to larger predators). By definition, these masks are located frontally. The malar stripes of falcons and the well-defined facial disks of owls are potential visual signals, perhaps serving the same function as the 'bandit' masks of racoons (*Procyon lotor*) and other carnivores. However, we see no obvious or logical relationship between the presence of ocelli in the nape and a warning to larger predators, mainly because the ocelli would not be visible during a confrontation. When approached by a predator (including humans), a falcon or owl always faces it, bobbing the head with erected feathers and striking with their talons if the attacker gets close enough (G. R. Bortolotti, J. J. Negro & J. H. Sarasola, pers. observ.).

THE FALSE FACE AS A PREDATORY AID

Unlike the previous category of hypotheses, there is only one potential type of receiver of the signal (i.e. small avian prey). There is ample evidence that raptors are often mobbed by the same species that they typically hunt. The mobbing response is often viewed as being evolutionary justified by the fact that mobbers want to chase away predators that may kill their kin or themselves. The necessary preconditions for these hypotheses to be supported are: (1) the inclusion of mobbing birds in the predator's diet or (2) the predator mimics a species that is subjected to mobbing.

Hypothesis 5: mobber manipulation

Some raptors may exploit what appears to be an innate response of mobbing birds against owls (Hinde, 1954a, b). Using models, Hinde demonstrated that owl shapes with frontal eyes are the most powerful releasers of mobbing responses. Owls are likely feared as nocturnal predators of roosting birds but, on the other hand, may not be agile enough during the day to retaliate. The alarm reactions of small birds are said to be very different toward falcons and hawks than toward owls (i.e. by fleeing, seeking cover and keeping a distance to the former) (Sparks & Soper, 1989). By mimicking an owl, a diurnal bird of prey may attract potential prey within a closer range and facilitate the hunt.

Alternative to enticing small birds closer, ocelli may put mobbers in a different position relative to the predator. The experiments by Deppe *et al*. (2003) described above are highly suggestive of a predatory function to ocelli. If passerines normally attack an owl from behind, but are deceived into attacking it frontally, the raptor is in a much better position to strike. Mobbers regularly pass within a few centimetres, and may actually strike raptors, and so their exact position relative to the predator influences risk dramatically.

Hypothesis 6: mobber census

This is a novel hypothesis and differs from the previous one in that mobbing is elicited by the predator to gain information about the types and abundance of potential prey in the area. Because the mobbing response is more intense in the vicinity of nest sites and when there are nestlings (Shields, 1984; Heinrich, 1987; G. R. Bortolotti, J. J. Negro & J. H. Sarasola, pers. observ.), the predator may obtain information about the presence of nestlings and fledglings, which are typically easier prey than adults. It may be difficult to test such an hypothesis because the benefit to the raptor may not be immediately obvious; however, it may help explain the settlement and movement patterns of raptors.

AN ANALYSIS OF GLAUCIDIUM

The large number of species in this nearly worldwide genus (del Hoyo *et al.*, 1999) allows the investigation of patterns patterns in the detectability of the signal and attributes of the birds that are consistent with the predictions of each hypothesis (Table 1). We searched the literature broadly for all available information on these species, and so our morphological and ecological data were derived from a variety of sources including major reviews (Voous, 1989; del Hoyo *et al.*, 1999; König *et al.*, 1999; Johnsgard, 2002) as well as books on local avifauna worldwide. Unfortunately, little is known of the biology and behaviour of many species. As a result, our quantitative analysis was restricted to body size and the use of general categories for habitat (open, open forest and forest, dense forest), and birds in the diet (high, moderate, low). Because the morphological data for most species were presented as ranges, we use the mid point in the range for wing length, and the low end for mass. The latter would be indicative of males, which are not going to vary as much females (e.g. over the breeding season). For heuristic purposes, we treat species as individual units, recognizing, however, that they are not phylogenetically independent. The taxonomy within this group is currently in flux.

Of 32 species, 24 have ocelli/false faces. Species with and without ocelli are distinct in size because there is only nominal overlap (Fig. 2). On average (mean ± SE), species without ocelli weighed (115.5 ± 11.9 g, $N = 8$) twice as much as species with ocelli (56.3 ± 1.5 g, $N = 24$).

Pygmy-owls can be found in a broad range of habitats and eat a diversity of foods; however, the two habits do not appear to be independent. Eight of ten (80%) species predominantly preying on birds were found in habitats described as open or open forest whereas ten of 14 (71%) species with only a low proportion of birds in the diet were found in forest or dense forest. To describe a species in general terms, we assigned each a three-point score for decreasing openness of habitat and decreasing proportion of birds in diet (see above). The sum score represents a scale from birds in open habitats to dense forest dwellers that do and do not eat birds, respectively. Birds with false faces decrease in frequency along this continuum whereas those without them increase (Fig. 3). It is interesting to note that although some species with ocelli are found in the forested extreme of the scale, the reverse was not true. It should be noted that the heights of the bars in Figure 3 are contingent on phylogeny; however, the general trend for populations of pygmy-owls with false faces to be characterized as open-country predators of birds would remain. The same conclusion can be reached by reviewing species descriptions (del Hoyo *et al.*, 1999).

DISCUSSION

All hypotheses presented in this review are logical constructs, and have not been deduced from actual field observations of the ocelli ‘in action’. There are no available data for any species to demonstrate that the ocelli influence the fitness of their bearers. However, we believe this kind of review, broadening the perspective on what may be plausible, is necessary to bring to light different predictions concerning the potential function of the ocelli, and may help researchers to design experiments and test our hypotheses. The same

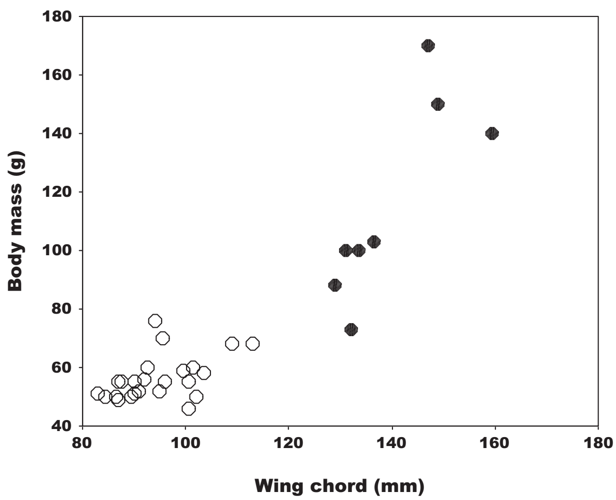

Figure 2. Wing chord length and body mass for *Glaucidium* pygmy-owls. Solid circles are species without ocelli and open circles have ocelli.

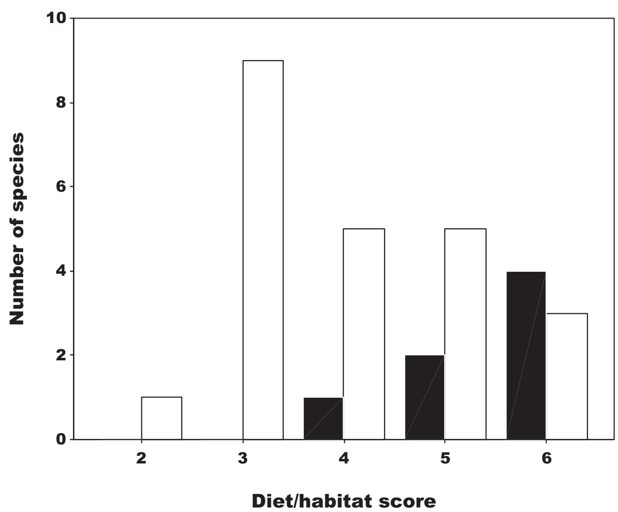

Figure 3. Distribution of species of *Glaucidium* pygmy-owls along a scale of open habitat species that eat birds (2) to dense forest species that do not eat birds (6).

approach has been used to deal with, what were at the time, puzzling traits such as avian mobbing (Curio, 1978a, b), alarm signals (Klump & Shalter, 1984a, b), the stotting in gazelles (Caro, 1986), and the pelage patterns of carnivores (Ortolani, 1999; Newman *et al*., 2005). Ocelli may have different functions depending on context or species, and hence some of the hypotheses are not mutually exclusive (Table 1).

Support for the antipredator or antimobber category of hypotheses is that the predatory birds displaying false faces are typically small and thus more vulnerable if struck. However, there are several lines of evidence that cast some doubt on this interpretation. The distinction between species with and without ocelli was particularly striking for *Glaucidium* (Fig. 2). The difference in size, although relatively large, may not be enough in absolute terms to alter risk from predators because most raptors are far larger than both types of owls. It is well known that owls that feed on pygmy-owls also prey on even larger owl species (Forsman *et al*., 2004). Larger size as a protective value against mobbers is also likely to be of marginal value. For example, using data on body masses of 3352 species from Dunning (1993), the mean pygmy-owl without ocelli would be heavier than 95.0% of passerines. However, even at half that mass, owls with ocelli are still heavier than 84.3% of passerines. We believe that such a large difference in size associated with ocelli is more likely to be explained by foraging ecology than a mere risk of mobbing. Smaller owls may have ocelli because they are faster and more agile, and thus more likely to be effective predators of birds (which could include mobbers). Generally, raptors specializing in killing passerines are small (see size distributions in *Falco* and *Accipiter*). The mobber manipulation hypothesis is the only one that links plumage to agility (Table 1). The small size of *Glaucidium* owls does not deter them from killing birds as large or larger than themselves (Steyn, 1979; Mikkola, 1983; del Hoyo *et al*., 1999; König *et al*., 1999; Holt & Petersen, 2000; Proudfoot & Johnson, 2000), and they have been observed to kill mobbers (Finch-Davies & Kemp, 1980; Fry, Keith & Urban, 1988).

One difficulty for the protection hypotheses is that ocelli are often large, contrasted and symmetrical spots, which may actually increase detection (Forsman & Merilaita, 1999). Objects that are rounded in shape are more striking and easily seen and recognized (Scaife, 1976a, 1976b). At least to human eyes, they appear to increase conspicuousness (Hafner & Hafner, 1977). We agree with Zahavi & Zahavi (1997: 53) who considered the predator-avoidance hypothesis ‘an insult to the intelligence of predators’. Predators may be less likely to be ‘fooled’ than passerines because there appears to be an asymmetry between raptorial and nonraptorial birds in the degree to which each responds to models. For example, passerines are well known to mob stuffed raptors as well as crude wooden or plastic models (Hinde, 1954a, b; Curio, 1975; Deppe *et al*., 2003). In contrast, carved decoys have been used for centuries by humans to attract and hunt waterfowl, but these decoys are not generally attacked by birds of prey. Similarly, live bait is virtually a necessity in trapping raptors (G. R. Bortolotti, J. J. Negro & J. H. Sarasola, pers. observ.). Hawks, falcons and owls can be captured with the use of a large owl as a lure when they themselves mob. However, it is well known that live lures are considerably more effective in eliciting a mobbing attack than even taxidermy mounts, and crude models are totally ineffective (Bloom, 1987; Jacobs, 1996; G. R. Bortolotti, J. J. Negro & J. H. Sarasola, pers. observ.). Therefore, we think it is implausible that raptors would be fooled by ocelli of their own, or other species.

Although the conspicuousness of the ocelli works against the protection hypotheses, it supports those regarding ocelli as predatory aids. Furthermore, other components of the detectability of ocelli and attributes of the species are supported by predictions of the predatory aid hypotheses (Table 1). Across species, ocelli can be either hidden, or at least reduced, or permanently conspicuous, which is contrary to most of the protection hypotheses and consistent with the predatory aid hypotheses (Table 1). That ocelli can be hidden at will by many species may mean that individuals may decide to limit unwanted mobbing.

Predators with false faces tend to eat small birds, hence the preponderance within the Falconidae (note especially among passerine eaters such as *subbuteo*, *columbarius*, and *fasciinucha*) and within *Glaucidium* (Fig. 3). To aid raptors in foraging, these signals should be visible from a distance, and may be most effective from afar given their crude resemblance to a face. Most falcons, and ocelli-bearing pygmy-owls (Fig. 3), are associated with open habitats. The behaviour of these species should be equally important in broadcasting the signal. Falcons are well known for conspicuous perching. The same is true for many pygmy-owls with false faces. Many species of *Glaucidium* can be active in a broad range of hours throughout the day, although species with ocelli are noted as being diurnal (Bent, 1961; Steyn, 1979; Voous, 1989; Kullberg, 1995; del Hoyo *et al*., 1999). There are numerous anecdotes of diurnal hunting pygmy-owls acting in a conspicuous fashion, most commonly the habit of perching in exposed locations such as the tips of trees. When hunting mammals, Eurasian pygmy-owls sit motionless, low in trees but, when they hunt birds, they follow flocks high in the canopy (Kullberg, 1995). When diurnal species are not hunting, they are said to find thick foliage (Fry *et al*., 1988; Voous, 1989), stay hidden (König *et al*., 1999), or roost in cavities (König *et al*., 1999) or against a tree (Fry *et al*., 1988), as also described for species without ocelli when roosting. Most studies reviewing the genus make special note of how dense roosting is for the purpose of hiding from mobbers (e.g. Voous, 1989; König *et al*., 1999), and that pygmy-owls are mobbed if discovered at or disturbed from their roost (Voous, 1989; del Hoyo *et al*., 1999; König *et al*., 1999). Although it could be argued that conspicuous, diurnal raptors may need protection more, and so have ocelli, it is not clear then why such a trait should repeatedly appear in predators rather than prey species.

Although the mobber manipulation hypothesis has never been proposed for raptors, there are other presumed cases of deception of prey among animals. *Micrastur* forest falcons are said to vocally provoke a mobbing response in birds as a hunting technique (Smith, 1969). The use of attractants is illustrated by species of fish that lure smaller fish or arthropods into their mouths using appendages resembling flies. Some semiaquatic vipers are said to use the tips of their tails to deceive frogs into believing they are small worms (Wharton, 1960). Mobber attraction has been suggested as an explanation for the accipiter-like plumage colour and morphology of hawk cuckoos (*Cuculus* spp.); by being mobbed, they may census potential hosts for their parasitic eggs (del Hoyo, Elliot & Sargatal, 1997). McLean & Rhodes (1991) recognized the similarity between social parasites and predators in potentially provoking mobbing as a means of attracting or obtaining information about their victims.

The species showing ocelli typically display them at will, perch conspicuously, are diurnal, of small size, agile, and have a high proportion birds in their diet. This description fits well all predictions of the predatory aid hypotheses, but infrequently so or contrary to the predictions of the protection hypotheses (Table 1). However, because the available evidence is not yet conclusive, field experiments using models of raptors with and without ocelli are needed to distinguish among the hypotheses (Deppe *et al*., 2003). These models should be presented in a systematic way to mobbers, potential predators, and conspecifics. Also sorely needed is more information on how raptors hunt avian prey. Although diet composition is typically well known from the analysis of pellets and prey remains, actual observations of hunting episodes are scarce or go unreported.

ACKNOWLEDGEMENTS

The first two authors contributed equally to this paper. We thank Arantxa, of Grupo para la Recuperación de la Fauna Autóctona y su Hábitat (Grefa), for lending us a live hobby, and Lauren Bortolotti for comments on the manuscript. We are also indebted to the following museum curators for allowing access to specimens: Josefina Barreiro (Museo Nacional de Ciencias Naturales, Madrid), José Cabot (Estación Biológica de Doñana, Sevilla), Andrew Kitchener (Royal Museum of Scotland, Edinburgh), Leslie Jessop (Hancock Museum, Newcastle Upon Tyne), Allan J. Baker (Royal Ontario Museum, Toronto). G.R.B. was funded by the Natural Sciences and Engineering Research Council of Canada, J.H.S. was supported by a scholarship from Consejo Nacional de Investigaciones Cient'ficas y Técnicas de Argentina (CONICET), and J.J.N.'s travel was assisted by F. Hiraldo.

REFERENCES

Altmann SA. 1956. Avian mobbing and predator recognition. *Condor* **58:** 241–253.

Andersson MB. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Balgooyen TG. 1975. Another possible function of the American kestrel's deflection face. *Jack-Pine Warbler* **53:** 115–116.

Bent AC. 1961. *Life histories of North American birds of prey*. New York, NY: Dover Publications.

Bildstein KL. 1982. Responses of northern harriers to mobbing passerines. *Journal of Field Ornithology* **53:** 7–14.

Bloom P. 1987. Capturing and handling raptors. In: Pendleton BAG, Millsap BA, Cline KW, Bird DM, eds. *Raptor management techniques manual*. Washington DC: National Wildlife Federation. 99–123.

Burtt EH Jr. 1981. The adaptiveness of animal colors. *Bioscience* **31:** 723–772.

Cade TJ. 1982. *The falcons of the world*. Ithaca, NY: Cornell University Press.

Caro TM. 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. *Animal Behaviour* **34:** 663–684.

Clay WM. 1953. Protective coloration in the American sparrow hawk. *Wilson Bulletin* **65:** 129–134.

Cott HB. 1940. *Adaptive coloration in animals*. London: Oxford University Press.

Cramp S, Simmons KEL. 1977. *The birds of western Palearctic*. Oxford: Oxford University Press.

Curio E. 1975. The functional organisation of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. *Animal Behaviour* **23:** 1–115.

Curio E. 1978a. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Zeitschrift für Tierpsychologie* **47:** 175–183.

Curio E. 1978b. The adaptive significance of avian mobbing. II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constrains. *Zeitschrift für Tierpsychologie* **47:** 184–202.

Curio E, Regelmann K. 1985. The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Zeitschrift für Tierpsychologie* **69:** 3–18.

Deppe C, Holt D, Tewksbury J, Broberg L, Petersen J, Wood K. 2003. Effect of northern pygmy-owl (*Glaucidium gnoma*) eyespots on avian mobbing. *Auk* **120:** 765–771.

Dunning JB. 1993. *CRC handbook of avian body masses*. Bota Racon, FL: CRC Press.

Finch-Davies C, Kemp A. 1980. *The birds of prey of southern Africa*. Johannesburg: Winchester Press.

Flasskamp A. 1994. The adaptive significance of avian mobbing. V. An experimental test of the 'move on' hypothesis. *Ethology* **96:** 322–333.

Forsman D. 1999. *The raptors of Europe and the Middle East*. London: T & AD Poyser.

Forsman ED, Anthony RG, Meslow EC, Zabel CJ. 2004. Diets and foraging behaviour of northern spotted owls in Oregon. *Journal of Raptor Research* **38:** 214–230.

Forsman A, Merilaita S. 1999. Fearful symmetry: pattern size and asymmetry affects aposematic signal efficacy. *Evolutionary Ecology* **13:** 131–140.

Fry CH, Keith S, Urban EK. 1988. *The birds of Africa*, Vol. 3. London: Academic Press.

Hafner JC, Hafner MS. 1977. The cryptic occipital spot in the Accipitridae (Falconiformes). *Auk* **94:** 293–303.

Heinrich B. 1987. *One man's owl*. Princeton, NJ: Princeton University Press.

Hinde RA. 1954a. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*). I. The nature of the response, and an examination of its course. *Proceedings of the Royal Society of London Series B, Biological Sciences* **142:** 306–331.

Hinde RA. 1954b. Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*). II. *Proceedings of the Royal Society of London Series B, Biological Sciences* **142:** 331–358.

Holt DW, Petersen JL. 2000. Northern pygmy-owl. In: Poole A, Stettenheim P, Gill F, eds. *The birds of North America*. Philadelphia, PA: Academy of Natural Sciences.

del Hoyo J, Elliot A, Sargatal J. 1994. *Handbook of the birds of the world, vol. II: New World vultures to guineafowls* Barcelona: Lynx editions.

del Hoyo J, Elliot A, Sargatal J. 1997. *Handbook of the birds of the world, vol. IV: sandgrouse to cuckoos*. Barcelona: Lynx editions.

del Hoyo J, Elliot A, Sargatal J. 1999. *Handbook of the birds of the world, vol. V: barn-owls to hummingbirds.* Barcelona: Lynx editions.

Jacobs EA. 1996. A mechanical owl as a trapping lure for raptors. *Journal of Raptor Research* **30:** 31–32.

Jenkins AR, Wagner ST, Hoffman I. 1991. First breeding record of the taita falcon in South Africa. *Ostrich* **62:** 78.

Johnsgard PA. 2002. *North American owls: biology and natural history*, 2nd. edn. Washington, DC: Smithsonian Institution Press.

Klump GM, Shalter MD. 1984a. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. *Zeitschrift für Tierpsychologie* **66:** 189–205.

Klump GM, Shalter MD. 1984b. Acoustic behaviour of birds and mammals in the predator context. II. The functional significance and evolution of alarm signals. *Zeitschrift für Tierpsychologie* **66:** 206–226.

Koehler A. 1992. A kestrel to the sky. *Journal of Raptor Research* **26:** 201–206.

König C, Weick F, Becking J. 1999. *Owls: a guide to the owls of the world*. Tonbridge, UK: Pica Press.

Kullberg C. 1995. Strategy of the pygmy owl while hunting avian and mammalian prey. *Ornis Fennica* **72:** 72–78.

Maynard Smith J, Harper D. 2003. *Animal signals*. Oxford: Oxford University Press.

McLean IG, Rhodes G. 1991. Enemy recognition and response in birds. *Current Ornithology* **8:** 73–211.

Mikkola H. 1983. *Owls of Europe*. London: T & AD Poyser.

Mueller HC. 1971. Displays and vocalizations of the sparrow hawk. *Wilson Bulletin* **83:** 249–254.

Negro JJ, Grande JM, Sarasola JH. 2004. Do Eurasian hobbies (*Falco subuteo*) have 'false eyes' on the nape? *Journal of Raptor Research* **38:** 287–288.

Newman C, Buesching D, Wolff JO. 2005. The function of facial masks in 'midguild' carnivores. *Oikos* **108:** 623–633.

Ortolani A. 1999. Spots, stripes, tail tips and dark eyes: predicting the function of carnivore colour patterns using the comparative method. *Biological Journal of the Linnean Society* **67:** 433–476.

Ostreiher Royal. 2003. Is mobbing altruistic or selfish behaviour? *Animal Behaviour* **66:** 145–149.

Pavey CR, Smyth AK. 1998. Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Animal Behaviour* **55:** 313–318.

Petrie M, Halliday T, Sanders C. 1991. Peahens prefer peacocks with elaborate trains. *Animal Behaviour* **41:** 323–331.

Poiani A, Yorke M. 1989. Predator harassment: more evidence on the deadly risk. *Ethology* **83:** 167–169.

Proudfoot GA, Johnson RR. 2000. Ferruginous pygmy-owl. In: Poole A, Stettenheim P, Gill F, eds. *The birds of North America*. Philadelphia, PA: Academy of Natural Sciences.

Savalli UM. 1995. The evolution of bird coloration and plumage elaboration. A review of hypotheses. *Current Ornithology* **12:** 141–190.

Scaife M. 1976a. The response to eye-like shapes by birds. I. The effect of context: a predator and a strange bird. *Animal Behaviour* **24:** 195–199.

Scaife M. 1976b. The response to eye-like shapes by birds. II. The importance of staring, pairedness and shape. *Animal Behaviour* **24:** 200–206.

Schlenoff DH. 1985. The startle response of blue jays to *Catocala* (Lepidoptera: Noctuidae) prey models. *Animal Behaviour* **33:** 1057–1067.

Shields WM. 1984. Barn swallow mobbing: self-defence, collateral kin defence, group defence, or parental care? *Animal Behaviour* **32:** 132–148.

Smith NG. 1969. Provoked release of mobbing – a hunting technique of *Micrastur* falcons. *Ibis* **111:** 241–243.

Sordahl TA. 1990. The risks of avian mobbing and distraction behavior: an anecdotal review. *Wilson Bulletin* **102:** 349–352.

Sparks J, Soper T. 1989. *Owls: their natural and unnatural history.* New York, NY: Facts on File.

Steyn P. 1979. Observations on pearl-spotted and barred owls. *Bokmakierie* **31:** 50–60.

Svensson L, Grant PJ, Mullarney K, Zetterström D. 2000. *Collins bird guide*. London: Harper Collins Publishers.

Voous KH. 1989. *Owls of the northern hemisphere*. Cambridge, MA: MIT Press.

Walker DG. 1983. Golden eagle killing mobbing carrion crows. *British Birds* **76:** 312.

Wharton CH. 1960. Birth and behavior of a brood of cottonmouths, *Agkistrodon piscivorus piscivorus*, with notes on tail-luring. *Herpetologica* **16:** 125–129.

Wheeler BK. 2003. *Raptors of eastern north America*. Princeton, NJ: Princeton University Press.

Wink M, Sauer-Gürth H. 2004. Phylogenetic relationships in diurnal raptors based on nucleotide sequences of mitochondrial and nuclear marker genes. In: Chancelor RD, Meyburg BU, eds. *Raptors worldwide*. Berlin: World Working Group on Birds of Prey and Owls. 483–498.

Zahavi A, Zahavi A. 1997. *The handicap principle*. Oxford: Oxford University Press.