Colour morphs in the Collared Pygmy Owl *Glaucidium brodiei* are age-related, not a polymorphism

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Colour morph variation is widely observed in owls and several studies have described differences in life history traits among the morphs. Traditionally, Glaucidium owls are described as having two colour morphs, rufous and grey, which are supposedly independent of age or sex. During 2010–2012, nest boxes were set up in order to study the basic life history of Collared Pygmy Owls *Glaucidium brodiei*. We banded the population and followed some of the fledglings for nearly two years. Our results – in combination with data from museum specimens – clearly show that the colour morph in Collared Pygmy Owls is age-dependent, changing from the original fledgling plumage (2–3 months after hatching) to the rufous morph (4–7 months after hatching), and finally to the definitive grey plumage. Our results reject the long-standing polymorphism hypothesis for the pygmy owl. We conclude that the age of the birds should be considered before a colour polymorphism can be confirmed, especially in secretive nocturnal species. The case of within-species polymorphism might be overstated in Strigiformes.

Key words: coloration, polymorphism, plumage, Strigiformes, Strix aluco

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A polymorphism within a species refers to variation of inherent traits among conspecific individuals, irrespective of age or sex. Colour variation, among the most prominent type of polymorphism, is widely recorded in vertebrates such as birds (Roulin 2004a), lizards (Sinervo & Lively 1996, Sinervo *et al.* 2001) or frogs (Mann & Cummings 2012, Medina *et al.* 2013). The existence and maintenance of such polymorphisms is interesting in the context of natural or sexual selection (Gray & McKinnon 2007). Among non-passerine birds, Galliformes, Cuculiformes and Strigiformes are those most commonly recorded with colour polymorphism and the function of the polymorphism has been well investigated in some of these taxa (Galeotti *et al.* 2003, Roulin 2004a).

Several genera of Strigidae have been described as having two or three colour morphs, including the genera of Pygmy Owls *Glaucidium*, Scops Owls *Otus*, Wood Owls *Strix*, Little Owls *Athene* and Barn owls *Tyto* (del Hoyo *et al.* 1999, Duncan 2003, König *et al.* 2009). The best studied case among the owls is probably the Tawny Owl *Strix aluco*, where the occurrence and ratio of the different colour morphs has been recorded. The Tawny Owl shows two basic morphs, rufous and grey (Brommer *et al.* 2005, Galeotti & Cesaris 1996, Galeotti & Sacchi 2003, Piault *et al.* 2009), although intermediate forms are sometimes defined (Brommer *et al.* 2005, Galeotti & Sacchi 2003, Piault *et al.* 2009). Individuals of different morph may also differ in some of their life-history traits (e.g., reproductive success or parasitaemia; Brommer *et al.* 2005; Roulin 2004b).

Owl species from tropical and subtropical regions have been less frequently studied compared to those in temperate regions. Due to insufficient information for many of these nocturnal species, colour polymorphisms might be misidentified from different plumages of individuals differing in sex or age. Among the 29 (König et al. 2009) to 31 (del Hoyo et al. 1999, Duncan 2003) species of *Glaucidium* owls in the world, at least seven species have been described with two colour morphs (del Hoyo et al. 1999, Duncan 2003, König et al. 2009). According to the description, the colour morphs (rufous versus grey) of these owls are independent of age or sex, and these different morphs are thus considered a true polymorphism. This is, for example, suggested for the Collared Pygmy Owl Glaucidium brodiei, a tiny owl distributed throughout Oriental Asia (Figure 1A). Although fairly common in Taiwan, information on the basic ecology of this species is still scarce. Here, we present data on plumage colour in this species in relation to age and sex, and show that the long-lasting classification of this species as being colour polymorphic is erroneous.

METHODS

The study was conducted at the Lien-hua-chih Research Center in central Taiwan (23°55'40"N, 120°53'24"E; altitude ranged from 450 to 800 m). The main habitat in this region consists of original broadleaf forest and planted woodland (Cryptomeria-like Taiwania Taiwania cryptomerioides and Japanese Cryptomeria Cryptomeria japonica), occupying 65% and 30% of the total area, respectively. A total of 120 nest boxes, designed specifically for the Collared Pygmy Owl (dimensions of nest box: $15 \times 15 \times 25$ cm (L × W × H); diameter of entrance hole: 5 cm), were set up in both types of forest (60 nests in each type) in February 2010. The nest boxes were set up 3 to 8 m above the ground and 5 to 18 m apart. Nest boxes were visited weekly from 2010 to 2012. Once breeding was confirmed, we checked the nest box on 3 days per week until the young fledged. Owlets were banded with an aluminium ring at day 13 to 15 after hatching.

Owl recapture started from July 2010 onwards. Play-back equipment, consisting of a digital recorder (Sony PCM-D50) and speaker (Sampo TH-W901L), was used to attract the target individual by broadcasting the calls recorded from individuals in the same area. Birds were caught with bal-chatri traps, with 3 to 5 Japanese White-eyes *Zosterops japonica* as lures. Each captured individual was photographed and their plumage colour categorized as fledgling, rufous or grey morph. The fledgling morph is less barred and spotted, with absence of the occipital. The rufous morph includes orange and yellow hues. The grey morph shows dark brown and grey plumages. Each individual was weighed with a 100 g Pesola balance to the nearest 1 g and body mass was used to identify sex: in breeding

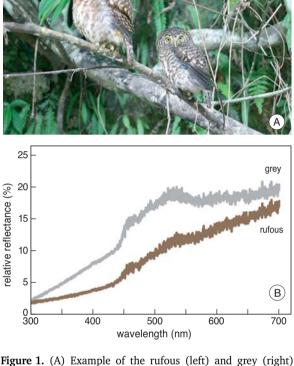


Figure 1. (A) Example of the rufous (left) and grey (right) plumage colour morph in the Collared Pygmy Owl in the field (photo taken on 27 November 2006, Nantou, central Taiwan, by W.-L. Lin). (B) Reflectance spectra of the spots on the head. The two morphs have similarly shaped reflectance spectra, but the overall reflectance of the spots of the grey morph is higher than that of the rufous morph.

pairs, males are always lighter than females (Brazil 2009). Because the ranges of male (52–72 g) and female (58–92 g) body mass overlap, the sex of floaters caught outside of the breeding season could only be identified when their body mass was outside the overlapping range.

Apart from the field study, we also reviewed a total of 68 specimens (24 male, 31 female, 13 no sex record) of the Collared Pygmy Owl from the National Museum of Natural Science (NMNS), the Biodiversity Research Center of Academia Sinica (BRCAS), the Taiwan Endemic Species Research Institute (TESRI), the Yamashina Institute for Ornithology (TIO) and the Wildlife Rescue and Conservation group of Taichung (WRCT; Appendix 1). For each specimen, we classified colour morph and noted the recorded sex and collection date. To provide a quantitative diagnosis of the colour of the rufous and grey morphs, we used a Jaz spectrometer (detection range: 250–800 nm, Ocean Optics, Inc., Dunedin, FL) connected to a reflection probe (ZFQ–13101, Ocean Optics, Inc.), which was lit by a deuterium–tungsten halogen light source (DH–2000–BAL, Ocean Optics, Inc.). We measured the colour of the spots on the head of five individual Collared Pygmy Owls (NMNS 00778, 00978, 00979, 1368 and 9525), by placing the probe vertically 2 mm above the focal part of the cuticle and adjusting it to obtain the maximal reflectance. We calibrated our measurements using a reflectance standard (Ocean Optics WS–1–SL).

RESULTS AND DISCUSSION

Between 25 May 2010 and 18 September 2012, we banded sixty-three Collared Pygmy Owls, including thirty-two nestlings, ten breeding adults and 21 floaters (age unknown). Seven nestlings were recaptured after fledging at least twice during the study period: their plumage colour changed from the fledgling to the rufous or the grey morph, depending on the time of recapture (Figure 2). One individual was recaptured four times and showed the sequential change from fledgling, to rufous to grey morph (Figure 3). This individual hatched on 15 June 2010 and fledged on 5 July. The first recapture was on 10 August, 56 days after it hatched, when it was fully grown, but still in the fledgling colour morph stage: the colour pattern was less barred and spotted on the back of the body and on top of the head, and the occipital was not formed completely (Figure 3B). The second recapture was on 27 November 2010, 165 days after hatching, and it was now in the rufous morph stage: the colour was orangered, barred on the back of the body and spotted on the top of the head, with the occipital formed (Figure 3B). The spots on the head were also larger at this stage (Figure 3B). The third and fourth recapture of this individual took place on 14 July 2011 (394 days after hatching) and on 5 June 2012 (720 days after hatching), respectively. In both recaptures, the owl showed the grey morph, with the whole body being grey (Figure 3C, D). The basal colour of the head looked grever when the bird was older (compare Figure 3C with 3D). Three other individuals (#3, 13 and 27) also exhibited a colour change from rufous to grey (Figure 2). These data clearly suggest that plumage colour is age-dependent and that the grey morph is the definitive plumage.

Among the 55 specimens with sex identification, 22 (40%) individuals were rufous and 33 (60%) were grey. The sex ratio of rufous (10 males and 12 females) and grey (19 male and 14 female) morphs did not show a significant difference ($X^2 = 0.78$; P = 0.38). The different morphs showed reflectance spectra that were similar in shape, but the total reflectance of the spots of the grey morph was higher than that of the rufous morph (Figure 1B).

Pooling the data from the museum specimens (56 with collection date) and the wild-caught individuals (including 10 breeders and 21 floaters) shows that the grey morph was more frequent than the rufous morph (66.7% *vs.* 33.3%) and appeared in every month. In contrast, the rufous morph was absent from May to July (Figure 4).

Based on our observations, we suggest that the colour morphs of the Collared Pygmy Owl should be defined as age plumages and not as a case of intraspecific colour polymorphism. The Collared Pygmy Owl exhibited fledgling plumage at two to three months after hatching, and became rufous at the age of four to seven months. The definitive plumage appeared when birds were ten to eleven months after hatching. Our breeding records from the nest boxes (Lin et al., unpublished data) showed that the Collared Pygmy Owls started to lay their eggs from late April to mid-June and fledged their young from early June to mid-August. These data are consistent with the temporal records from the museums, which indicate that the rufous morph appeared only after August, i.e. approximately two to four months after hatching.

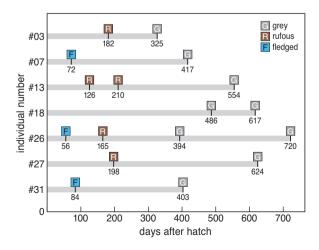


Figure 2. Colour morphs of seven free-living Collared Pygmy Owls that were recaptured at least twice after fledging in relation to individual age.

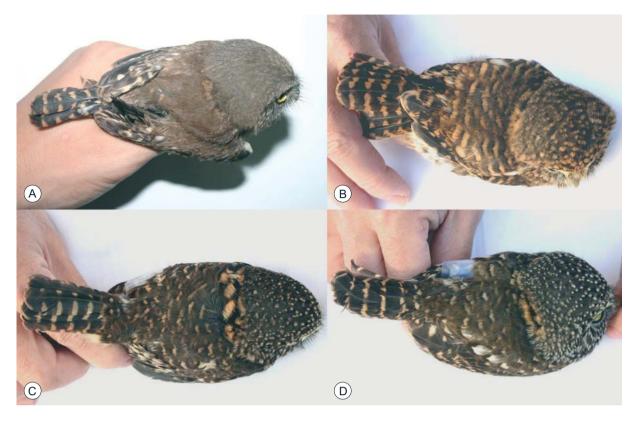


Figure 3. An example of the sequential change of colour morph with age in the Collared Pygmy Owl (number 26). Photos taken at the age of (A) day 56; (B) day 165; (C) day 394; and (D) day 720 after hatching.

Although the hypothesis that Collared Pygmy Owls are polymorphic was not supported in this study, the diversity of plumage colour expression in this species and in other Strigiformes is still noteworthy. For instance, both the Barn Owl and the Tawny Owl display a true adult polymorphism, but they also change their colouration during different life stages (Dreiss & Roulin 2010, Emaresi et al. 2013, Roulin et al. 2003). Both the true polymorphism and the age-dependent colour morphs may have evolved under variable selection pressures (Dreiss & Roulin 2010, Roulin et al. 2003). The Collared Pygmy Owl is extremely territorial and active day and night (Brazil 2009). The juvenile colour morph might thus help avoid aggressiveness from adults (VanderWerf & Freed 2003, Vergara & Fargallo 2007), but this requires further testing.

The results of this study reject the long-lasting idea that the Collared Pygmy Owl exhibits a true colour polymorphism. Considering the fact that most *Glaucidium* spp. are distributed in regions where even less research has been conducted, the existence of a colour polymorphism in the other six *Glaucidium* spp. is also doubtful. We suggest that the age of the owls should be considered before the existence of a colour polymorphism can be decided. We conclude that the frequency of within-species polymorphisms might be over-estimated in Strigiformes.

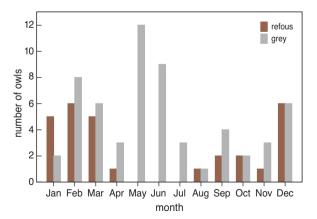


Figure 4. The number of rufous and grey morph specimens of the Collared Pygmy Owls in relation to the month at which they were collected (n = 56 museum specimens) or caught (n = 31 free-living individuals).

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SAMENVATTING

Bij uilen komt binnen een soort vaak variatie in kleur van het verenkleed voor (kleurpolymorfie). Verschillende studies hebben aangetoond dat deze variatie is geassocieerd met variatie in life-history eigenschappen. Gewoonlijk worden er bij uilensoorten van het geslacht Glaucidium twee kleurfasen beschreven, een roodbruine en een grijze. Meestal wordt ervan uitgegaan dat de kleurfasen niet afhangen van de leeftijd of het geslacht van de vogels. In een onderzoek aan een nestkastpopulatie van Gekraagde Dwerguilen Glaucidium brodiei dat in 2010-2012 in het Lien-hua-chih Research Center in Taiwan werd uitgevoerd, werd de polymorfie bij deze soort in kaart gebracht. De populatie werd geringd en de uitgevlogen jongen werden tot maximaal twee jaar daarna gevolgd. De resultaten - in combinatie met gegevens van museumexemplaren - laten duidelijk zien dat de kleurfasen bij de Gekraagde Dwerguil leeftijdsafhankelijk zijn. Tot 2-3 maanden na het uitkomen van de eieren hebben de uitgevlogen jongen allemaal hetzelfde verenkleed. Dit verandert in een roodbruin kleed (4-7 maanden na uitkomst). Uiteindelijk verandert dit in een grijs verenkleed. Deze resultaten ondermijnen de lang aangehangen gedachte dat veel soorten dwerguilen polymorf zijn. We concluderen dat er rekening met de leeftijd van vogels moet worden gehouden voordat een kleurpolymorfie wordt vastgesteld, met name bij heimelijke, nachtactieve soorten. Het voorkomen van kleurpolymorfie in uilen wordt derhalve mogelijk overschat. (PW)

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