The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2015, **116**, 134–143. With 3 figures.

Do rufous common cuckoo females indeed mimic a predator? An experimental test

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Received 2 February 2015; revised 31 March 2015; accepted for publication 31 March 2015

The similarity of common cuckoos *Cuculus canorus* to raptors is accepted as a classic example of predator mimicry. However, cuckoo females are polymorphic: grey females are similar to sparrowhawks *Accipiter nisus*, while rufous females were assumed to mimic kestrels *Falco tinnunculus*. Previous evidence based on dummy experiments with grey females consistently showed that both hosts and non-hosts recognize this brood parasite by its yellow eye and barred underparts. However, these traits are absent in kestrels. Host responses also do not covary geographically with local abundance of supposed models (sparrowhawks/kestrels). These patterns cast doubts on the kestrel-mimicry hypothesis. Here, we show experimentally for the first time that small birds that are unsuitable as hosts indeed do not mistake rufous cuckoos for kestrels: both tree sparrows *Passer montanus* and house sparrows *P. domesticus* feared grey cuckoos (similarly to sparrowhawks and kestrels) but ignored rufous cuckoos (similarly to innocuous Eurasian collared doves *Streptopelia decaocto*). These results provide further support for the hawk-mimicry hypothesis, but reject the kestrel-mimicry hypothesis. Colour polymorphism in birds is determined genetically, follows simple Mendelian rules and affects only colour but not patterns. These facts and striking similarities between plumages of rufous females and cuckoo fledglings suggest that the rufous morph is simply a colour alternative to the grey morph, did not evolve to mimic kestrels and might have arisen through paedomorphic retention of juvenile plumage to adulthood (neoteny). Research on the genetic, developmental and mechanistic basis of cuckoo plumage polymorphism will be especially revealing. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **116**, 134–143.

ADDITIONAL KEYWORDS: aggressive mimicry – apostatic selection – Batesian mimicry – colour polymorphism – delayed plumage maturation – frequency-dependent selection – neoteny – predator mimicry.

INTRODUCTION

Colour polymorphism, the co-occurrence of two or more distinct colour morphs within the same population, provides a striking example of phenotypic biodiversity under the influence of natural selection (Karpestam, Merilaita & Forsman, 2013). Therefore, it has fascinated biologists since the times of Darwin (1859) and has been the subject of intensive research. However, although colour polymorphism has been well documented in a variety of taxa (Roulin, 2004), the mechanisms underlying the evolution and maintenance of morphs remain poorly known. Classic examples include brood parasitic cuckoos. The disproportionally high frequency of plumage polymorphism in parasitic cuckoos was noted a half-century ago (Voipio, 1953; Payne, 1967), but experimental study of colour variation in this group is still in its infancy (for reviews see Thorogood & Davies, 2013; Trnka & Grim, 2013).

A suitable model species for studying colour plumage polymorphism in brood parasitic cuckoos is the common cuckoo *Cuculus canorus* (hereafter cuckoo) in which females occur in two distinct morphs (Voipio, 1953; Payne, 1967; Cramp, 1985; Davies, 2000; Erritzøe *et al.*, 2012). To the human eye, the grey female morph looks similar to the male Eurasian sparrowhawk *Accipiter nisus* (hereafter sparrowhawk) and a rufous female morph resembles the female Eurasian kestrel *Falco tinnunculus* (hereafter kestrel). Previous studies have hypothesized that these two morphs have arisen through apostatic

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*Corresponding author. E-mail: tomas.grim@upol.cz selection; such negative frequency-dependent selection would stem from rare morphs being less likely to be recognized by hosts than common morphs (Payne, 1967; Honza *et al.*, 2006).

However, recent experiments with both hosts and non-hosts have shown that to avian eyes the grey cuckoo morph successfully mimics the sparrowhawk ('hawk-mimicry'), which facilitates a parasite female's access to host nests (Davies & Welbergen, 2008; Welbergen & Davies, 2011). Further correlative evidence also supports the hawk-mimicry hypothesis: hawk-like features in cuckoos phylogenetically correlate with cuckoo polymorphism (Thorogood & Davies, 2013) and geographically correlate with sympatric raptor models (Gluckman & Mundy, 2013). This suggests that mimicry dynamics may promote evolution and maintenance of multiple female morphs in parasitic cuckoos (Thorogood & Davies, 2012, 2013). However, whether the rufous female morph represents frequency-dependent mimicry for an additional model, most probably the kestrel ('kestrel-mimicry': Voipio, 1953), or only represents an alternative phenotypic variant of the grey morph, remains unresolved.

To date, several studies have tested the significance and effectiveness of hawk-mimicry in both host and non-host species (Honza *et al.*, 2006; Davies & Welbergen, 2008; Welbergen & Davies, 2011; Trnka & Prokop, 2012; Trnka, Prokop & Grim, 2012; Trnka & Grim, 2013, 2014b), but only one experimental study has also focused on kestrel-mimicry (Trnka & Grim, 2013). However, results from that study failed to reveal any functional significance of cuckoo–kestrel resemblance probably due to the high aggressiveness of the tested host species, the great reed warbler *Acrocephalus arundinaceus*. Although great reed warblers recognized grey cuckoos from sparrowhawks, they did not discriminate between rufous cuckoos and kestrels, attacking both with the same intensity. That predator hawk-mimicry is not effective against this highly aggressive host has also been demonstrated previously both experimentally (Honza *et al.*, 2006; Trnka & Prokop, 2012; Trnka & Grim, 2013, 2014b; see also Liang & Møller, 2014) and through observations of great reed warblers killing female cuckoos at this host's nests at various study sites (Molnár, 1944; Janisch, 1948; Trnka & Grim, 2013; Mérő & Žuljević, 2014). Thus, a more revealing test of the kestrel-mimicry hypothesis might be one on a less aggressive host and especially on small passerines with no history of cuckoo parasitism (see Davies & Welbergen, 2008).

We adopted the experimental design of Davies & Welbergen (2008), who tested the hawk-mimicry hypothesis on cuckoo-naïve bird species (great tits *Parus major* and blue tits *Cyanistes caeruleus* in their study; hereafter tits) by using taxidermic stuffed dummies presented at feeders outside the breeding season when there is zero risk (due to cuckoo migratory habits) that immediate host responses would be confounded by concurrent cuckoo activity in the study area (see Davies & Welbergen, 2009). Therefore, in the present study also we used non-host species: Eurasian tree sparrows *Passer montanus* and house sparrows *Passer domesticus* (hereafter sparrows). Just like tits, sparrows represent suitable model species because they also breed in holes, and thus are primarily unsuitable (*sensu* Grim *et al.*, 2011) as cuckoo hosts (hole-nesters are parasitized extremely rarely and thus did not coevolve with cuckoos; Grim *et al.*, 2014). Both species of sparrows feed in open spaces (mainly on the ground), and thus are exceptionally vulnerable to attack from predators (see supplementary materials in Møller *et al.*, 2012). Both species are regular parts of the diet of sparrowhawks (Møller *et al.*, 2012) and kestrels (Kübler, Kupko & Zeller, 2005). However, sparrowhawks are more dangerous than kestrels during both the breeding season and winter (Tvardíková & Fuchs, 2012). Sparrowhawks specialize in killing small passerines (Møller *et al.*, 2012), while kestrels feed both on passerines and more commonly on mammals (Kübler *et al.*, 2005). This pattern makes our predictions more specific (see below). We tested sparrow responses towards all protagonists of hawk- and kestrel-mimicry, i.e. grey and rufous cuckoos, sparrowhawks and kestrels, and a harmless control, the Eurasian collared dove *Streptopelia decaocto* (hereafter collared dove).

In general, mimicry hypotheses predict that signal receivers (sparrows in our case) confuse mimic with its model, i.e. observers respond similarly to both mimic and model (Grim, 2005a; Davies & Welbergen, 2008). Specifically, the hawk-mimicry hypothesis predicts that observers confuse grey cuckoos with highly dangerous sparrowhawks, i.e. fear both at similarly high levels. The kestrel-mimicry hypothesis predicts that observers confuse rufous cuckoos with relatively less dangerous kestrels, i.e. avoid both at similar levels that are lower than fear showed to sparrowhawks.

METHODS

Study species

Both Eurasian tree sparrows and house sparrows are obligatory social birds, visit feeders in flocks and are often numerically dominant over other species (Liker & Barta, 2002; Barta, Liker & Mónus, 2004). Sparrows were almost exclusive users of the feeders (see below) in the present study too: only occasionally did we record other species, specifically the great tit ($N = 16$), blue tit ($N = 9$), coal tit *Periparus ater* ($N = 2$), common blackbird *Turdus merula* ($N = 4$), European robin *Erithacus rubecula* ($N = 1$) and collared dove ($N = 8$). Similarly to previous studies (e.g. Davies & Welbergen, 2008) we did not record or analyse responses of such marginal species.

Out of 1925 observed sparrows, Eurasian tree sparrows were more common (80.4%) than house sparrow (19.6%). Flock size varied from seven to 31 individuals ($N = 102$ flocks). Each flock was mixed, i.e. containing at least one individual from either species. There were no obvious differences in the behaviour of the two species. Indeed, removing data from less common house sparrow (i.e. analysing only data from more common Eurasian tree sparrow: $N = 102$ flocks, 1547 observed birds) had minimal effect on parameter estimates and did not change any of our conclusions (results not shown). Therefore, we pooled data from the two focal species, as in previous studies of avian anti-predator behaviour at feeders (e.g. Davies & Welbergen, 2008; Tvardíková & Fuchs, 2011, 2012).

Sparrows feed mostly on the ground, but seek shelter in trees and bushes. They show typical feeding behaviour: individuals arrive to a spot in a tree or bush, observe the feeder and its surroundings for a while from a distance, and only then (presumably after they perceive the space around the feeder is safe) the flock flies down to the feeder. In contrast to tits, sparrows do not fly away with the food, but consume it directly on the feeder. Individual birds fly repeatedly between the arrival point in a tree or bush and the feeder. The immediate risk of predation significantly affects their feeding strategies: when threatened, they visit a feeder in smaller flocks, spend far less time on it and are more vigilant, decreasing the frequency of flights and, consequently, their vulnerability (Barta *et al.*, 2004; Trnka & Prokop, 2006).

EXPERIMENTAL DESIGN

Experiments were conducted during the winters (December–February) of 2013/2014 and 2014/2015. We used three spatial replicates, i.e. three feeders: two at the edge of Trnava city (48°21′36″N, 17°35′27″E and 48°21′49″N, 17°35′29″E) and one in Majcichov village (48°16′48″N, 17°37′45″E), south-west Slovakia. The feeders were positioned in private gardens, planted with a mixture of coniferous and deciduous (mainly fruit-bearing) trees and bushes. The feeders were ~2 m away from the closest tree. Trees surrounding the feeders served as a shelter and observation place for sparrows. The feeders were made of rectangular board (1.0 × 0.8 m) with raised edges to avoid food scattering, and fixed to four 1.2-m-long vertical poles. To attract the birds, feeders were exposed minimally 2 weeks before the first experimental series and filled daily with sunflower and millet seeds (2:1).

Each trial consisted of presenting a single stuffed dummy, either of the grey cuckoo (female), rufous cuckoo (female), sparrowhawk (small female), kestrel (female) or collared dove (this species does not show sexual dimorphism or dichromatism; innocuous control: Grim, 2005b; Trnka *et al.*, 2012). Dummies were stuffed in life-like position and were made and maintained in good condition by the same experienced taxidermist (A.T.). We used three replicates (specimens) per each dummy type. At each study site, the dummy was fixed to a spruce branch at a distance of ~6 m from the edge of the feeder (at a height of ~1.8 m) and faced toward the feeder. On each experimental day dummies of only three types were used. Types and their sequence within each series of trials were arranged randomly. Each experimental day started 1 h after daybreak. There were 4–5 days breaks between experimental days, depending on immediate weather conditions.

Each trial began with the observers (A.T. and M.T.) approaching the feeder and refilling it with food, which resulted in flushing the birds away from the vicinity. Then the observers positioned the dummy (see above) and retreated to a hiding place located 10 m away. After birds returned to the vicinity of the feeder, their responses were recorded. Each trial lasted for 5 min from arrival of the first individual to the feeder (following Davies & Welbergen, 2008). Sparrows show a specific feeding behaviour compared with other feeder visitors (see above), so we recorded the following behavioural variables: the total number of birds in the flock that arrived in the vicinity of the feeder (to the closest tree) before flying to the feeder or flying away from the tree without feeding (this variable was recorded to calculate another behavioural variable, the percentage of active birds at the feeder, see below, and it was not used in subsequent statistical analyses); the latency from arrival of the first individual to the tree to arrival of the first bird to the feeder; flight frequency (total number of bird arrivals at and departures from the feeder during 5 min from the arrival of the first flock member at the feeder); and the percentage of active birds feeding at the feeder (calculated as the percentage of the maximum number of individuals observed at the feeder out of the total number of birds, see above, per the same 5 min). Simultaneously, the following weather parameters were also recorded: temperature (continuous, to the nearest degree), wind (continuous, according to Beaufort scale, 0 = calm to 6 = strong breeze) and cloudiness (according to an ordinal scale from 1 = the sky was clear to 4 = sky was completely cloudy). We modelled ‘wind’ as a continuous predictor only after verifying that it was not statistically significant when modelled as an ordinal predictor (following Grafen & Hails, 2002).

Sparrows feed in flocks and are very active, preventing a reliable determination of all individually colour-banded individuals. Therefore, to quantify the rate of pseudoreplication (i.e. re-testing the same individuals), sparrows were trapped using mist-nets after all trials on the particular day were finished. Each bird was individually banded with a unique combination of colour rings. Altogether, 266 sparrows were caught during 17 trapping days throughout both winters. However, only 4–6% of birds were re-captured on a different day on the three respective feeders, suggesting a very low rate of pseudoreplication (lower than in previous studies, e.g. Davies & Welbergen, 2008; Tvardíková & Fuchs, 2011).

STATISTICAL ANALYSES

We analysed the data ($N = 102$ for all analyses) following Honza *et al.* (2010). We $\log_{10}$-transformed latency to arrival to successfully normalize it. Latency strongly negatively correlated with both flight frequency ($r_s = -0.40$, $P < 0.0001$) and percentage of active birds ($r_s = -0.86$, $P < 0.0001$). In turn, flight frequency correlated strongly positively with percentage of active birds ($r_s = 0.51$, $P < 0.0001$). Therefore, we performed principal components analysis (PCA). We further used only principal component PC1 that complied with Kaiser’s criterion (Eigenvalue > 1). PC1 had an Eigenvalue of 2.07 (i.e. it explained 69% of the variation) and correlated negatively with latency ($r_s = -0.92$, $P < 0.0001$) and positively with percentage active birds ($r_s = 0.92$, $P < 0.0001$) and flight frequency ($r_s = 0.64$, $P < 0.0001$). Although our statistical analyses were based on PC1, we also present raw data (Table 1) to show original variation per each parameter of sparrow behaviour that cannot be seen from PC1 only. Not including the raw estimates would prevent including the present study into future meta-analyses.

The full model explaining variation in sparrow behaviour (PC1) included the major predictor of interest (dummy type) and weather predictors (temperature, wind and cloudiness). We checked whether there was collinearity (assessed by the variance inflation factor, VIF) between all predictors, following the procedures recommended by Zuur, Ieno & Elphick (2010). We found no evidence of collinearity (all predictors showed VIFs < 2: Zuur *et al.*, 2010).

To test for potential clustering in the data we included ‘season’ (nominal: 2013/2014 vs. 2014/2015), ‘day’ (continuous, centred by year: Grim *et al.*, 2011), ‘daytime’ (continuous, Central European Time hour), ‘feeder’ (nominal, three levels) and ‘dummy id’ (nominal, three levels per each dummy type) as random effects. We modelled all of them as random because we had no specific directional predictions for these potential confounders (modelling all these potential confounders as fixed predictors led to identical conclusions). However, all these random effects explained negligible variation (< 2%) and their 95% confidence intervals (CIs) widely overlapped zero. Indeed, the full model without these random effects or any of their subset combinations had much better fit (assessed by Akaike information criterion corrected for small sample size, $\mathrm{AIC_c}$); also, parameter estimates, both from full and final models, remained quantitatively the same with or without these random effects or any of their subset combinations (assessed by 95% CIs). Therefore, we removed these redundant random effects as recommended by Bolker *et al.* (2009).

Table 1. Variation in responses to various dummies by house and Eurasian tree sparrows (both species pooled, see Methods); shown are median and range because the raw data did not conform to a normal distribution

Dummy type	*N*	Latency to arrival (s)	Flight frequency (no.)	Percentage of active birds (%)
Collared dove	17	5 (2–30)	3 (1–7)	92 (79–100)
Cuckoo – grey	21	55 (10–300)	2 (0–12)	18 (0–67)
Sparrowhawk	19	80 (20–300)	1 (0–5)	12 (0–48)
Cuckoo – rufous	23	10 (5–40)	4 (1–9)	82 (50–100)
Kestrel	22	35 (15–300)	3 (0–8)	44 (0–80)

We used sequential backward elimination of non-significant terms from the full model (Grafen & Hails, 2002). For readers’ convenience, we present results of both the full and the final model to show that presenting the full model (as recommended by Forstmeier & Schielzeth, 2011) or minimum adequate (final) model (as recommended by Grafen & Hails, 2002) does not affect our conclusions. Model residuals followed a normal distribution in both the full and the final models as assessed by both visual inspection (Grafen & Hails, 2002) and Shapiro–Wilk tests ($W = 0.96$ and 0.97).

To objectively assess a relative weight of evidence in favour of the hawk-mimicry vs. kestrel-mimicry hypotheses we calculated standardized effect sizes (d) for sparrow responses to grey cuckoos vs. sparrowhawks and to rufous cuckoos vs. kestrels, respectively (following Lipsey & Wilson, 2001).

All tests were two-tailed. All analyses were done in JMP 11.0.0. (SAS Institute). All values are presented as mean ± SE.

RESULTS

Sparrows showed high variation in responses both within and between dummies (Table 1). Dummy type had a strong effect on sparrow responses (Fig. 1) regardless of whether the weather covariates were included (full model) or sequentially excluded (minimum adequate model; Table 2). In other words, weather variables did not explain any significant variation in sparrow responses (Table 2). Post-hoc comparisons [Tukey honest significant difference (HSD), see Fig. 1] showed that sparrows responded similarly to grey cuckoos, sparrowhawks and kestrels; these responses were characterized by long latencies to arrival, low percentage of active birds and low flight frequencies. Such fearful responses did not statistically differ between grey cuckoos and kestrels, while responses to sparrowhawks were even more timid than those to grey cuckoos and kestrels (Fig. 1). In contrast, responses to rufous cuckoos and collared doves were different (and statistically similar to each other); these responses were characterized by short latencies to arrival, high percentage of active birds and high flight frequencies (Fig. 1). Thus, responses to the grey cuckoo and its model (the sparrowhawk) were in the same direction (Fig. 1), and although the difference reached statistical significance, the standardized effect size was relatively small ($d = 0.77$). In contrast, responses to the rufous cuckoo and its model (the kestrel) were in the opposite direction (Fig. 1), and statistically significantly different with much larger effect size ($d = 2.67$).

DISCUSSION

Sparrows exhibited fine-tuned discrimination of various dummies near the feeder as shown by their responses as either fear (late arrival of a low number of birds at the feeder and their low activity) or ignorance of the dummy (early arrival of a high number of birds at the feeder and their high activity). Most importantly, sparrows responded differently to grey cuckoos, which they feared, than to rufous cuckoos, which they ignored. Responses were in the similar direction (i.e. timid) to the grey cuckoo and its sparrowhawk model, with statistically even more fearful responses to sparrowhawks compared with grey cuckoos. In contrast, responses to the rufous cuckoo were similar to responses to the innocuous control collared dove while responses to its model (i.e. kestrel) were instead more similar to grey cuckoo and sparrowhawk. These patterns show that grey cuckoo mimicry was effective, eliciting fear in sparrows. In contrast, rufous cuckoos mimicry (if any, see further) was not effective, eliciting ignorance in sparrows. As predicted, responses to kestrels (less dangerous raptors: Kübler *et al.*, 2005) were less fearful than responses to sparrowhawks (more dangerous raptors: Møller *et al.*, 2012; Fig. 1). The significant difference between sparrow responses towards grey cuckoo and sparrowhawk dummies suggests, on the other hand, also that this cuckoo morph does not mimic the predator model perfectly, most probably because it lacks certain important features of raptors, such as hooked beak and claws. A

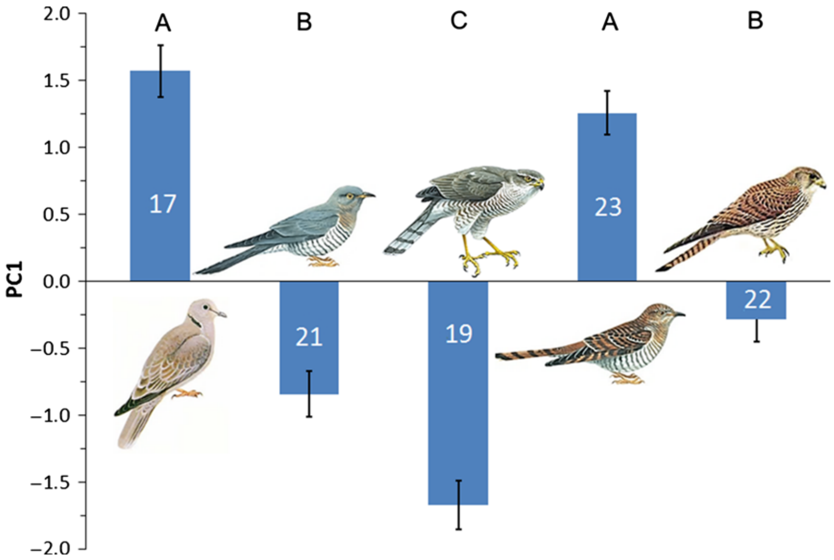

Figure 1. Sparrow responses (mean ± SE) to enemy and control dummies near feeders. Behaviour was summarized by PCA (see Methods). Negative values of PC1 indicate that birds arrived later and showed less activity (flight frequency), and a lower percentage of present birds actively dared to approach the feeder. Estimates are from the final model (Table 1). Letters above bars indicate significant differences between treatments (dummy types) according to Tukey HSD post-hoc tests ($\alpha = 0.05$). Sample sizes for each dummy are given in bars.

Table 2. Sparrow responses to dummy types near their feeder; responses were quantified as PC1 from PCA on latency to arrival, flight frequency and percentage active birds (see Methods)

		Full model		Final model	
Predictor	d.f.	*F*	*P*	*F*	*P*
Dummy	4	55.47	< 0.0001	59.23	< 0.0001
Temperature	1	0.14	0.71		
Wind	1	0.00	0.99		
Cloudiness	3	1.02	0.39		

Full model: $F_{9,92} = 26.16$, $P < 0.0001$, adjusted $R^2 = 0.69$; the final model: $F_{4,97} = 59.23$, $P < 0.0001$, adjusted $R^2 = 0.70$. For estimates see Figure 1.

similar pattern has also been found for a suitable and currently used cuckoo host species, the great reed warbler (Trnka & Prokop, 2012; Trnka & Grim, 2013).

Thus, sparrow responses supported the hawk-mimicry hypothesis, but not the kestrel-mimicry hypothesis (see also standardized effect sizes in the Results). These conclusions could not be confounded by sparrows' experience, either immediate or long-term: cuckoos are migratory and not present in the study area during winter, whereas both sparrowhawks and kestrels are regularly present in the study area year-round (own observations).

Batesian or aggressive mimicry?

Most studies refer to cuckoo vs. hawk/falcon similarity as Batesian mimicry (e.g. Honza *et al.*, 2006; Thorogood & Davies, 2012; Gluckman & Mundy, 2013; Trnka & Grim, 2013). However, an alternative view is that cuckoo–raptor similarity does not represent Batesian mimicry but aggressive mimicry (Wyllie, 1981; Welbergen & Davies, 2011; Stoddard, 2012; see also Mappes & Lindström, 2012). Specifically, Batesian mimics resemble dangerous models to avoid predation, i.e. Batesian mimicry is defensive. Aggressive mimics, by contrast, falsely threaten dupes with predation.

In contrast to previous literature we suggest that it may be more fruitful to consider two separate groups of cuckoo hosts, for each of which the cuckoo would represent a different type of mimicry (though we acknowledge that the two types may rather represent the ends of a single continuum, just as mimetic and non-mimetic eggs are not categories but ends of a continuum: Grim, 2005a).

Batesian mimicry may apply to those of cuckoo hosts that are fearless and do not get threatened by intruders. Such hosts are even able to kill the cuckoo, e.g. red-backed shrikes *Lanius collurio* (Yoshino, 1999) and great reed warblers (above). In other words, aggressive mimicry would not work for these super-aggressive hosts: both red-backed shrikes and great reed warblers fearlessly attack any intruders near their nests and do not flee from them (see references above).

Aggressive mimicry may apply to those of cuckoo hosts that are fearful and escape from (at least some) intruders. Such hosts are easily threatened. This group includes some small cuckoo hosts that escape approaching cuckoos and do not dare to physically attack them, e.g. reed warblers (Moksnes *et al.*, 2000) or redstarts (Rutila, Latja & Koskela, 2002; Grim *et al.*, 2009).

An additional point-of-view not considered in previous studies takes into account another relevant dupe: not host adults but predators of adult cuckoos (Payne, 1967). According to this view, adult cuckoos mimic raptors to avoid predation by them. Indeed, cuckoos form a dramatically and spatially consistently smaller proportion of prey of both sparrowhawks and goshawks *Accipiter gentilis* than expected from the cuckoo's abundance in the breeding bird community (Møller *et al.*, 2012).

These considerations suggest that future studies of predator mimicry in cuckoos need to incorporate additional parameters (e.g. risks of sparrowhawk and goshawk predation on adult cuckoos). Further, Batesian mimicry and aggressive mimicry scenarios should not be viewed as exclusive alternatives but as complementary explanations with varying importance in different cuckoo hosts that vary in their responses towards cuckoos from fearless to fearful.

Polymorphism does not need to be mimetic to thwart host defences

The mechanistic basis of cuckoo plumage and hawk–cuckoo similarity is unknown (cf. known mechanistic basis of cuckoo egg mimicry: Igic *et al.*, 2012). In general, colour plumage polymorphism in birds is determined genetically, follows simple Mendelian inheritance rules and – crucially – affects only colour but not patterns (Roulin, 2004). Taken together, this suggests that rufous females may simply represent a colour alternative to grey females and did not evolve to mimic kestrels. This conclusion is supported by experimental evidence that consistently showed that recognition cues used by both cuckoo hosts and non-hosts are yellow eye (iris) and barred underparts, i.e. traits absent in kestrels (Fig. 2; Davies & Welbergen, 2008; Trnka *et al.*, 2012; Trnka & Grim, 2013) and by strikingly different responses of non-hosts to rufous cuckoos and kestrels (this study).

Hawk-like traits of cuckoos correlate geographically with hawk-like traits of sympatric raptor models

Figure 2. Plumage patterns on the body underparts and eye colour (i.e. discrimination cues used by bird observers) in grey cuckoo female, sparrowhawk, rufous cuckoo female and kestrel female (from left to right).

(Gluckman & Mundy, 2013). However, host responses do not covary geographically with local abundance of sparrowhawks and kestrels (Trnka & Grim, 2013). For human eyes, rufous females may be even more similar to merlins *Falco columbarius* than kestrels (Voipio, 1953). Yet the rufous morph typically lives in allopatry with merlins, contrary to an assumption that rufous females mimic merlins (see also Gluckman & Mundy, 2013). This provides another independent line of evidence against a hypothesis that rufous females are mimicking falconid raptors.

Under an apostatic selection scenario, hosts form by learning an avoidance image for the colour morph that is currently more common (Davies & Welbergen, 2009). Ancestors of parasitic cuckoos were parental cuckoos that were monomorphic (Krüger, Davies & Sorenson, 2007). Therefore, we can assume that grey females represent an ancestral state (adult male cuckoos are always grey), while rufous cuckoos represent a derived condition. Importantly, to effectively disrupt host learning of the commoner morph (the original grey morph) the alternative new morph (i.e. the rufous one) did not need to mimic any new model. All that was needed for the new morph to be effective (from the parasite's point-of-view) was that it differed from the original morph. The maintenance of both morphs (grey mimetic and rufous non-mimetic) was then realized through apostatic selection based on dynamic assessment of current danger by hosts (Thorogood & Davies, 2012; see also Trnka & Grim, 2014a). In general, similarity (e.g. superficial similarity between rufous cuckoos and kestrels) does not imply mimicry (Grim, 2005a, 2013; Prum, 2014).

DID THE RUFOUS FEMALE MORPH ARISE THROUGH NEOTENY?

Thorogood & Davies (2012, 2013) suggested that the rufous cuckoo morph evolved after the grey morph's effectiveness declined due to host learning. Then the frequency of two morphs would be subject to negatively frequency-dependent selection, with any currently rarer morph gaining advantage through its rareness and, consequently, lowered opportunity for hosts to learn its appearance and to adjust their responses. But if the rufous morph is not merely an alternative colour morph but specifically mimics the kestrel (Voipio, 1953) then its frequency should logically reflect the frequency of the model, i.e. kestrel (see also Prum, 2014). However, this prediction is not supported: the frequency of rufous/grey cuckoo morphs does not correlate with the frequency of kestrel/sparrowhawk models and host responses are stronger to the locally commoner cuckoo morph regardless of the local presence/absence of kestrels and sparrowhawks (Trnka & Grim, 2013). These correlative data, coupled with experimental data (this study), reject the hypothesis that the rufous cuckoo morph is mimicking kestrels.

Indeed, a closer look at the external phenotype of cuckoo morphs and their assumed models is in line with the hawk-mimicry hypothesis but does not support the kestrel-mimicry hypothesis (Fig. 2). Sparrowhawks and grey cuckoos share underpart barring and yellow eyes (iris), both of which are important discrimination cues for hosts (Davies & Welbergen, 2008; Trnka *et al.*, 2012; Gluckman & Mundy, 2013). Additionally, they share grey head and upperparts (Stoddard, 2012) although the adaptive significance of these similarities has not yet been tested experimentally. We also note that the grey cuckoo female is more similar to the sparrowhawk male than to the female: see the rusty tint on the grey cuckoo female neck (which is a primary visual trait that allows human observers to recognize cuckoo females from males: Cramp, 1985). In contrast, kestrels and rufous cuckoo females do not share either underpart patterns (spotted in kestrel vs. barred in rufous cuckoo) or eye colour (black in kestrel vs. yellow in rufous cuckoo, see Fig. 2). Additionally, upperpart patterns are also different: spotted in kestrel vs. barred in rufous cuckoo females.

Without the experimental evidence presented in this study, one could argue that relatively poor similarity of rufous female cuckoos to kestrels represents a case of imperfect mimicry (Grim, 2005a,b, 2013; Harper &

Figure 3. Overall appearance of grey cuckoo female, rufous cuckoo female and young cuckoo fledgling (from left to right).

Pfennig, 2007). In general, selection does not fine-tune the model-mimic similarity in cases when the model is very dangerous – only a rough similarity is sufficient to force avian observers to err on the safe side (Prum, 2014). However, kestrels are less dangerous to small passerines than are sparrowhawks, predicting opposite patterns than those observed in reality. This provides another line of circumstantial evidence against the kestrel-mimicry hypothesis.

In summary, all these correlative dissimilarity patterns and experimental data consistently do not provide any support for the kestrel-mimicry hypothesis in cuckoos. Instead, the rufous morph is strikingly similar to a young cuckoo (Fig. 3): the extent of barring across the head, neck, upperparts and underparts is virtually the same in rufous females and fledglings; in contrast, grey females do not show any barring on the head or upperparts and only faint and limited barring on the front and sides of the neck (as is obvious from any bird field guide or published photographs). Notably, both rufous female patterns and background colours are much more similar to those in young birds than to both patterns and colours of adult grey females (Fig. 3).

Therefore, we suggest a new hypothesis that the rufous female morph may have arisen due to a paedomorphic process of neoteny (for examples of partial neoteny in birds see: Björklund, 1991; Doucet *et al.*, 2007). As far as we know, individual development of cuckoo plumage remains unknown, and thus there is also a possibility that ageing rufous females later develop grey plumage (delayed plumage maturation: Foster, 1987). Either way, we envisage that research on the genetics of cuckoo plumage, its mechanistic basis and its development will be central to our understanding of cuckoo plumage polymorphism.

ACKNOWLEDGEMENTS

In this research we followed guidelines of the Animal Behavior Society for the ethical use of animals in research. Licences and permission to ring and handle the birds were provided by the Ministry of Environment of the Slovak Republic, No. 269/132/05-5.1pil and No. 7230/2008-2.1pil. We thank N. B. Davies for perceptive comments on a previous version of the manuscript. We also thank three anonymous reviewers and A. Sternalski for their helpful comments. When working on the manuscript, T.G. was supported by Human Frontier Science Program awards RGY69/07 and RGY83/12 and grant no. P506/12/2404 from the Czech Science Foundation.

REFERENCES

Barta Z, Liker A, Mónus F. 2004. The effects of predation risk on the use of social foraging tactics. *Animal Behaviour* **67:** 301–308.

Björklund M. 1991. Coming of age in fringillid birds: heterochrony in the ontogeny of secondary sexual characters. *Journal of Evolutionary Biology* **4:** 83–92.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* **24:** 127–135.

Cramp S, ed. 1985. *Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 4. Terns to Woodpeckers*. Oxford: Oxford University Press.

Darwin CR. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Davies NB. 2000. *Cuckoos, cowbirds and other cheats*. London: T. & A. D. Poyser.

Davies NB, Welbergen JA. 2008. Cuckoo–hawk mimicry? An experimental test. *Proceedings of the Royal Society of London B* **275:** 1817–1822.

Davies NB, Welbergen JA. 2009. Social transmission of a host defense against cuckoo parasitism. *Science* **324:** 1318–1320.

Doucet SM, McDonald DB, Foster MS, Clay RP. 2007. Plumage development and molt in long-tailed manakins (*Chiroxiphia linearis*): variation according to sex and age. *Auk* **124:** 29–43.

Erritzøe J, Mann CF, Brammer FP, Fuller RA. 2012. *Cuckoos of the world*. London: Christopher Helm.

Forstmeier W, Schielzeth H. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology* **65:** 47–55.

Foster M. 1987. Delayed maturation, neoteny, and social system differences in two manakins of genus *Chiroxiphia*. *Evolution* **41:** 547–558.

Gluckman TL, Mundy NI. 2013. Cuckoos in raptors' clothing: barred plumage illuminates a fundamental principle of Batesian mimicry. *Animal Behaviour* **86:** 1165–1181.

Grafen A, Hails R. 2002. *Modern statistics for the life sciences*. Oxford: Oxford University Press.

Grim T. 2005a. Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not? *Biological Journal of the Linnean Society* **84:** 69–78.

Grim T. 2005b. Host recognition of brood parasites: implications for methodology in studies of enemy recognition. *Auk* **122:** 530–543.

Grim T. 2013. Mimicry, signalling, and co-evolution. *Ethology* **119:** 270–277.

Grim T, Rutila J, Cassey P, Hauber ME. 2009. The cost of virulence: an experimental study of egg eviction by brood parasitic chicks. *Behavioral Ecology* **20:** 1138–1146.

Grim T, Samaš P, Moskát C, Kleven O, Honza M, Moksnes A, Røskaft E, Stokke BG. 2011. Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? *Journal of Animal Ecology* **80:** 508–518.

Grim T, Samaš P, Procházka P, Rutila J. 2014. Are tits really unsuitable hosts for the common cuckoo? *Ornis Fennica* **91:** 166–177.

Harper GR, Pfennig DW. 2007. Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? *Proceedings of the Royal Society of London B* **274:** 1955–1961.

Honza M, Šicha V, Procházka P, Ležalová R. 2006. Host nest defense against a color-dimorphic brood parasite: great reed warblers (*Acrocephalus arundinaceus*) versus common cuckoos (*Cuculus canorus*). *Journal of Ornithology* **147:** 629–637.

Honza M, Procházka P, Šicha V, Požgayová M. 2010. Nest defence in a cuckoo host: great reed warblers risk themselves equally for their own and parasitic chicks. *Behaviour* **147:** 741–756.

Igic B, Cassey P, Grim T, Greenwood DR, Moskát C, Rutila J, Hauber ME. 2012. A shared chemical basis of avian host–parasite egg colour mimicry. *Proceedings of the Royal Society of London B* **279:** 1068–1076.

Janisch M. 1948. Fight between *Cuculus c. canorus* L. – cuckoo – and *Acrocephalus a. arundinaceus* L. – great reed warbler. *Aquila* **55:** 291.

Karpestam E, Merilaita S, Forsman A. 2013. Detection experiments with humans implicate visual predation as a driver of colour polymorphism dynamics in pygmy grasshoppers. *BMC Ecology* **13:** 17.

Krüger O, Davies NB, Sorenson MD. 2007. The evolution of sexual dimorphism in parasitic cuckoos: sexual selection or coevolution? *Proceedings of the Royal Society of London B* **274:** 1553–1560.

Kübler S, Kupko S, Zeller U. 2005. The kestrel (*Falco tinnunculus* L.) in Berlin: investigation of breeding biology and feeding ecology. *Journal of Ornithology* **146:** 271–278.

Liang W, Møller AP. 2014. Hawk mimicry in cuckoos and anti-parasitic aggressive behavior of barn swallows in Denmark and China. *Journal of Avian Biology* **46:** 216–223.

Liker A, Barta Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. *Behaviour* **139:** 1061–1076.

Lipsey MW, Wilson DB. 2001. *Practical meta-analysis*. Beverly Hills, CA: Sage.

Mappes J, Lindström L. 2012. How did the cuckoo get its polymorphic plumage? *Science* **337:** 532–533.

Mérő TO, Žuljević A. 2014. Great reed warbler *Acrocephalus arundinaceus*. *Acrocephalus* **34:** 130.

Moksnes A, Røskaft E, Hagen LG, Honza M, Mørk C, Olsen PH. 2000. Common cuckoo *Cuculus canorus* and host behaviour at reed warbler *Acrocephalus scirpaceus* nests. *Ibis* **142:** 247–258.

Møller AP, Solonen T, Byholm P, Huhta E, Nielsen JT, Tornberg R. 2012. Spatial consistency in susceptibility of prey species to predation by two *Accipiter* hawks. *Journal of Avian Biology* **43:** 390–396.

Molnár B. 1944. The cuckoo in the Hungarian Plain. *Aquila* **51:** 100–112.

Payne R. 1967. Interspecific communication signals in parasitic birds. *American Naturalist* **101:** 363–385.

Prum RO. 2014. Interspecific social dominance mimicry in birds. *Zoological Journal of the Linnean Society* **172:** 910–941.

Roulin A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews* **79:** 815–848.

Rutila J, Latja R, Koskela K. 2002. The common cuckoo *Cuculus canorus* and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? *Journal of Avian Biology* **33:** 414–419.

Stoddard MC. 2012. Mimicry and masquerade from the avian visual perspective. *Current Zoology* **58:** 630–648.

Thorogood R, Davies NB. 2012. Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. *Science* **337:** 578–580.

Thorogood R, Davies NB. 2013. Hawk mimicry and the evolution of polymorphic cuckoos. *Chinese Birds* **4:** 39–50.

Trnka A, Grim T. 2013. Color plumage polymorphism and predator mimicry in brood parasites. *Frontiers in Zoology* **10:** 25.

Trnka A, Grim T. 2014a. Dynamic risk assessment: does a nearby breeding nest predator affect nest defence of its potential victim? *Journal of Ethology* **32:** 103–110.

Trnka A, Grim T. 2014b. Testing for correlations between behaviours in a cuckoo host: why do host defences not covary? *Animal Behaviour* **92:** 185–193.

Trnka A, Prokop P. 2006. Do predators cause a change in passerine movement patterns as indicated by mist-net trapping rates? *Ardea* **94:** 71–76.

Trnka A, Prokop P. 2012. The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. *Animal Behaviour* **83:** 263–268.

Trnka A, Prokop P, Grim T. 2012. Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? *PLoS ONE* **7:** e37445.

Tvardíková K, Fuchs R. 2011. Do birds behave according to dynamic risk assessment theory? A feeder experiment. *Behavioral Ecology and Sociobiology* **65:** 727–733.

Tvardíková K, Fuchs R. 2012. Tits recognize the potential dangers of predators and harmless birds in feeder experiments. *Journal of Ethology* **30:** 157–165.

Voipio P. 1953. The hepaticus variety and the juvenile types of the cuckoo. *Ornis Fennica* **30:** 97–117.

Welbergen JS, Davies NB. 2011. A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioral Ecology* **22:** 574–579.

Wyllie I. 1981. *The cuckoo*. London: Batsford.

Yoshino T. 1999. *Kakko – Nihon no takurancho*. Tokyo: Bunichisogoshuppan.

Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1:** 3–14.