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Author for correspondence:

Knud Andreas Jönsson
e-mail: kajonsson@snm.ku.dk

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The evolution of mimicry of friarbirds by orioles (Aves: Passeriformes) in Australo-Pacific archipelagos

Knud Andreas Jönsson^{1,2}, Kaspar Delhey^{3,4}, George Sangster^{5,6}, Per G. P. Ericson⁵ and Martin Irestedt⁶

¹Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, 2100 Copenhagen Ø, Denmark

²Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

³School of Biological Sciences, Monash University, Clayton Campus, Clayton, 3800 Victoria, Australia

⁴Max Planck Institute for Ornithology, Radolfzell 78315, Germany

⁵Department of Zoology, and ⁶Department of Bioinformatics and Genetics, Swedish Museum of Natural History, PO Box 50007, Stockholm 10405, Sweden

Observations by Alfred Wallace and Jared Diamond of plumage similarities between co-occurring orioles (*Oriolus*) and friarbirds (*Philemon*) in the Malay archipelago led them to conclude that the former represent visual mimics of the latter. Here, we use molecular phylogenies and plumage reflectance measurements to test several key predictions of the mimicry hypothesis. We show that friarbirds originated before brown orioles, that the two groups did not co-speciate, although there is one plausible instance of co-speciation among species on the neighbouring Moluccan islands of Buru and Seram. Furthermore, we show that greater size disparity between model and mimic and a longer history of co-occurrence have resulted in a stronger plumage similarity (mimicry). This suggests that resemblance between orioles and friarbirds represents mimicry and that colonization of islands by brown orioles has been facilitated by their ability to mimic the aggressive friarbirds.

1. Introduction

Species may resemble each other in appearance for various reasons. For example, closely related species may not have had sufficient time to diverge phenotypically, or convergence may lead to a similar appearance across distantly related species. This could have developed in the course of millions of years either by random chance or because a given design (shape or colour) is favoured in a particular habitat or environment. Alternatively, mimicry may increase the resemblance of one species (mimic) to another (the model), thereby leading to an advantage for the mimic or for both species [1,2].

Interspecific social dominance mimicry (ISDM) is a proposed form of social parasitism in which a subordinate species evolves to mimic and deceive a dominant ecological competitor to avoid attack by the dominant model species. Among the roughly 10 000 species of birds, there may be about 50 phylogenetically independent origins of visual ISDM (reviewed by Prum [3]), and game-theoretic models have shown the plausibility of this hypothesis [4]. However, few of these putative cases have been investigated in detail.

Wallace [5] was the first, to the best of our knowledge, to describe visual mimicry between orioles (*Oriolus*, Oriolidae) and friarbirds (*Philemon*, Meliphagidae) in the Moluccan islands. He suggested that orioles could avoid attack by hawks by mimicking the aggressive friarbirds. Stresemann [6] disputed the mimicry claim, which he thought was simply the result of convergent evolution ("*Resultat unabhängiger Convergenz der Entwicklungsrichtungen*"). More recently, Diamond [7] provided a detailed account of the various explanations of the mimicry between orioles and friarbirds and based on field observations suggested that orioles *do* mimic the friarbirds to avoid attack from the friarbirds when feeding in the

same fruiting trees. Diamond [7] also noted that the similarities between orioles and friarbirds must represent a case of mimicry and *not* convergence, because field evidence suggested that the smaller orioles benefit from mimicking the larger pugnacious friarbirds. Consequently, Wallace and Diamond both believed that orioles mimic friarbirds but provided two different explanations for the origin.

The oriole–friarbird study system is remarkable because it includes multiple species pairs, which show different degrees of plumage similarity [7]. This provides an excellent setting for studying the evolution of visual mimicry. While both Wallace and Diamond spent years in the field to understand the mimicry of orioles and friarbirds, they could only base their conclusions on observations, distributional data and anecdotal evidence but had no tools to investigate when and where the two species groups evolved relative to each other. Molecular phylogenetic data provide the means to address these questions. Recent studies have suggested that brown orioles originated in Australo-Papua and subsequently dispersed to the Wallacean archipelago [8]. Friarbirds also appear to have originated in the Australo-Papuan region [9–11] with subsequent colonizations of the Wallacean and Pacific archipelagos. However, taxon sampling for friarbirds has been incomplete, and here we present a comprehensive, dated phylogenetic framework including both groups. Because human and avian perceptions of colours differ [12], we also quantify the patterns of colour similarity between orioles and friarbirds based on spectrometric measurements of reflectance of museum specimens and analyse these measurements using psychophysical models of avian colour vision [13].

In this study, we integrate molecular data, morphological data and plumage similarity for orioles (*Oriolus*) and friarbirds (*Philemon*) to address questions pertaining to the evolution of mimicry. We explicitly assess the predictions of the ISDM model set forth by Prum [3]. We also assess how coexistence times of models and mimics have affected mimicry, expecting that mimicry improves the longer orioles and friarbirds have coexisted. Finally, we assess the diversification of orioles and friarbirds in space and time to ask when the mimetic group originated relative to the model group and also specifically tested if brown orioles and friarbirds co-specified.

2. Material and methods

(a) Taxon sampling

We included the molecular data from 53 individuals of 30 out of 32 taxa (all 18 species) of the genus *Philemon* (missing *P. buceroides ammitophilus* from interior Australia and *P. novaeguineae trivialis* from the north coast of southeast New Guinea) and 40 individuals of all 17 taxa (eight species) of brown orioles (*Oriolus*) following the International Ornithological Congress World Bird List v. 5.1 [14] (electronic supplementary material, table S1). To root the trees, we also included four additional outgroup taxa for *Oriolus* following Jønsson *et al.* [8] and four outgroup taxa for *Philemon* following Andersen *et al.* [11]. We sequenced the mitochondrial gene ND2 for all individuals and included two nuclear markers (GAPDH and ODC) for three species of brown orioles and one nuclear marker (Fib-5) for 11 species of friarbirds.

(b) Phylogenetic and dating analyses

DNA sequences were aligned for each gene individually using MAFFT [15] and subsequently checked in SEAVIEW [16]. Each

of the four gene partitions (ND2, GAPDH, ODC and Fib-5) were then analysed separately in BEAST [17] applying the most appropriate model of nucleotide evolution as determined by MODELTEST v. 3.7 [18] following the Akaike information criterion (AIC). Analyses were run for 20 million generations using a relaxed uncorrelated lognormal distribution for the molecular clock model and assuming a Yule speciation process for the tree prior.

We then analysed the concatenated datasets for *Philemon* (ND2 and Fib-5) and *Oriolus* (ND2, GAPDH and ODC) independently. These analyses were run for 100 million generations (sampling every 1000 generations) using a relaxed uncorrelated lognormal distribution for the molecular clock model and assuming a birth–death speciation process for the tree prior. We used two nucleotide substitution partitions for *Oriolus* and three nucleotide substitution partitions for *Philemon* applying the most appropriate model of nucleotide evolution as determined by MODELTEST v. 3.7 [18] following the AIC. Finally, we analysed ND2 for both *Philemon* and *Oriolus* combined using a relaxed uncorrelated lognormal distribution for the molecular clock model and assuming a birth–death speciation process for the tree prior. To obtain absolute dates, we applied to our data a rate of 0.0145 substitutions per site per lineage (2.9%) per Myr [19]. We used default prior distributions for all other parameters and ran Markov chain Monte Carlo chains for 100 million generations sampling every 1000th generation to produce a posterior distribution of 100 000 trees.

All analyses were repeated multiple times, and convergence diagnostics were assessed using TRACER [20] checking that effective sample size values for all parameters were higher than 200, suggesting little autocorrelation between samples. Output trees were summarized using TREEANNOTATOR [21] as a maximum clade credibility (MCC) tree after discarding 25% of generations as burn-in.

(c) Ancestral state reconstruction

We used LAGRANGE [22,23] to estimate ancestral areas within *Oriolus* and *Philemon*. We assigned three geographical areas for the LAGRANGE analysis: (i) Australo-Papua, (ii) Wallacea (islands west of New Guinea), and (iii) the Pacific (islands east of New Guinea). We randomly selected 1000 trees from the posterior distribution of the BEAST analysis of the concatenated dataset and ran LAGRANGE on each of these trees. The frequency of the most likely ancestral areas for clades was plotted as marginal distributions on the MCC tree derived from the BEAST analysis, recording the area (max. areas = 2) with the highest relative probability for each node.

(d) Friarbird–brown oriole co-speciation

We tested the strength of evolutionary associations between co-occurring friarbirds and orioles by using the function ‘ParaFit’ [24] implemented in the R package ‘ape’ [25] in R v. 3.1.2 [26]. The null hypothesis is that the two phylogenies and the set of co-occurrence links have diversified independently.

(e) Colour resemblance between orioles and friarbirds

We quantified plumage similarity between orioles and friarbirds using spectrometric measurements from museum specimens and visual models. Reflectance spectra were collected using a Avaspec 2048 spectrometer connected to a AvaLight-XE pulsed xenon light source (Avantes, Eerbeek, The Netherlands) through a bifurcated fibre-optic cable. The measuring probe was fitted with a black plastic cylinder (6 mm inner diameter) to standardize measuring distance (5 mm) and exclude ambient light, which was held perpendicular to the plumage (coincidental normal, [27]). We collected the reflectance spectra from 18 standardized plumage patches: front, crown, dorsal neck, upper back, lower back, rump, dorsal tail proximal, dorsal tail distal, lores, cheek, wing

scapulars, wing primaries, throat, ventral neck, upper breast, lower breast, belly and vent (electronic supplementary material, figure S1). Specimens were measured at the British Museum of Natural History in Tring, UK. We measured one to six specimens per species (average = 3.8, s.e. = 0.26; see electronic supplementary material, table S2 for a list of specimens) for 137 specimens and 38 taxa at subspecies level (14 orioles and 24 friarbirds, see electronic supplementary material), totalling 2457 reflectance spectra. Reflectance spectra (300–700 nm, the visual sensitivity range of most birds, [12]) were expressed relative to a WS-2 white standard (Avantes). For the analyses, we pooled the data from male and female specimens.

Differences in coloration between orioles and friarbirds were assessed using psychophysical models of avian vision [13], computing chromatic and achromatic contrast between homologous plumage patches for each oriole–friarbird pair (for further details on visual models, see electronic supplementary material, figure S2). Chromatic contrasts quantify the differences in hue and saturation between homologous patches while achromatic contrasts quantify differences in brightness (light to dark). For each sympatric oriole–friarbird pair, we averaged all chromatic contrasts, and all achromatic contrasts computed between homologous plumage patches and combined these into a new variable (colour contrast) following [28] (for more details, see the electronic supplementary material).

Chromatic and achromatic contrasts were computed following Vorobyev *et al.* [13] and Siddiqi *et al.* [29], respectively. Given that oriole mimicry is thought to be aimed at deceiving friarbirds, we used visual sensitivity functions for V-type birds [30], the most likely visual system for friarbirds [31]. Similarly, to compute noise-to-signal ratios (using a Weber fraction of 0.05 and formula 9 in [13], we used the average cone proportions (0.41 : 0.77 : 1.01 : 1; VS : S : M : L) of the only two species in the family for which there are data (*Entomyzon cyanotis* and *Manorina melanocephala* [32]). Sensitivity functions for double cones are not known to vary between species, and we used the sensitivity spectrum of *Leiothrix lutea* and a Weber fraction of 0.05 [29]. Finally, we used the spectrum of standard daylight (D65) as illuminant [13]. Visual models were run in the R environment [26], using the scripts in Delhey *et al.* [33] (for further details, see the electronic supplementary material).

(f) Statistical analyses

Diamond [7] suggested that the greater the size difference between the model and the mimic, the better the plumage mimicry. Another aspect that appears relevant is the time of co-occurrence. If orioles mimic friarbirds, then one would hypothesize that the mimicry improves the longer orioles and friarbirds have coexisted. Size differences were computed as the ratio between oriole and friarbird tarsus length. K.A.J. measured the length of the tarsus for one to eight specimens (in total, 65 specimens) of 24 out of 32 taxa of *Philemon* and one to five specimens (in total, 36 specimens) of 15 out of 17 taxa of brown orioles (electronic supplementary material, table S3). Coexistence time was taken as the youngest divergence time to the nearest sister taxon of any given co-occurring oriole–friarbird pair (e.g. for *Philemon moluccensis* and *Oriolus boroensis* that coexist on the island of Buru, the age of the oriole is 2.13 Myr as this is the estimated age of the node of common ancestry between this taxon and its sister taxon. Similarly, the age of the friarbird is 2.67 Myr. Thus, the time of coexistence is set at the youngest of the two time estimates at 2.13 Myr). We used generalized-linear models to assess the potential effects of size difference and coexistence time on colour contrast. In all cases, we fitted three models: one for each independent variable in separate models and one for both variables together including the interaction term. These analyses were first carried out, using all sympatric oriole–friarbird pairs as independent data points

($n = 33$ for coexisting time and $n = 30$ for size difference owing to missing morphological data on *Philemon c. corniculatus*). We also used generalized-linear models to assess whether colour contrast, size differences and coexistence times varied geographically (between the three regions in which orioles and friarbirds co-occur: Wallacea, New Guinea and Australia).

These analyses, using all oriole–friarbird pairs, have two drawbacks: some oriole taxa contribute more than one data point to the analyses, and phylogenetic relatedness is not accounted for. Hence, for those oriole taxa with multiple sympatric friarbirds, we averaged colour contrast values to obtain a single taxon-specific value ($n = 14$ oriole taxa). We then fitted phylogenetic generalized-linear models with function ‘pgls’ as implemented in the R package ‘caper’ [34], using the oriole phylogeny depicted in figure 1. These models estimate Pagel’s lambda, a parameter that indicates the degree of phylogenetic correlation in the data and statistically accounts for it using suitable branch length transformations [36]. As mentioned above, these models included those testing for the separate effects of size difference and coexistence time and for their effects in interaction. We did not test for regional differences using this approach owing to low number of oriole taxa in some areas (New Guinea).

The values of colour contrast computed provide us an indication of the absolute levels of contrast between orioles and friarbirds. If oriole plumage has evolved to match that of sympatric friarbirds, then we expect that values of colour contrast between orioles and sympatric friarbirds should be lower compared with colour contrast values between orioles and allopatric friarbirds. To quantify this, we computed for each oriole taxon ($n = 14$) the average colour contrast with sympatric and allopatric friarbirds and compared them using a phylogenetic paired *t*-test [37] as implemented in the R package ‘phytools’ [38] using the oriole phylogeny depicted in figure 1. Negative values of paired differences would indicate that orioles are better mimics of sympatric than allopatric friarbirds. Similar to the phylogenetic generalized-linear models mentioned above, this test estimates lambda and adjusts results accordingly.

3. Results

(a) Phylogenetic relationships and taxonomy

Analysis of the mitochondrial ND2 gene produced a phylogeny for brown orioles and friarbirds (figure 1 and electronic supplementary material, S3), which is almost fully congruent with the phylogenies for friarbirds and orioles based on both mitochondrial and nuclear data (electronic supplementary material, figures S4–S5), with only minor differences for poorly supported nodes. The two subspecies of *O. melanotis* (*O. m. melanotis* and *O. m. finschi*) differ by 6.4% in mitochondrial DNA, which is similar to differences between several other species of brown orioles. Also, *O. decipiens* represents a distinct lineage, which is not closely related to *O. boroensis* as previously suggested [35,39]. The two species of brown orioles of Australo-Papua with five (*O. sagittatus*) and six (*O. flavocinctus*) subspecies are both monophyletic and subspecies are largely indistinguishable in the molecular analysis. Three species of friarbirds (*P. novaeguineae*, *P. buceroides* and *P. citreogularis*) are not monophyletic and may include multiple valid species.

(b) Timing, origin and dispersal of friarbirds and orioles

Ancestral area analyses are not able to unambiguously identify a particular region as the origin for brown orioles and friarbirds (figure 1). Other analyses with a broader taxon sampling have suggested that the origin is likely Australo-Papuan [8–11].

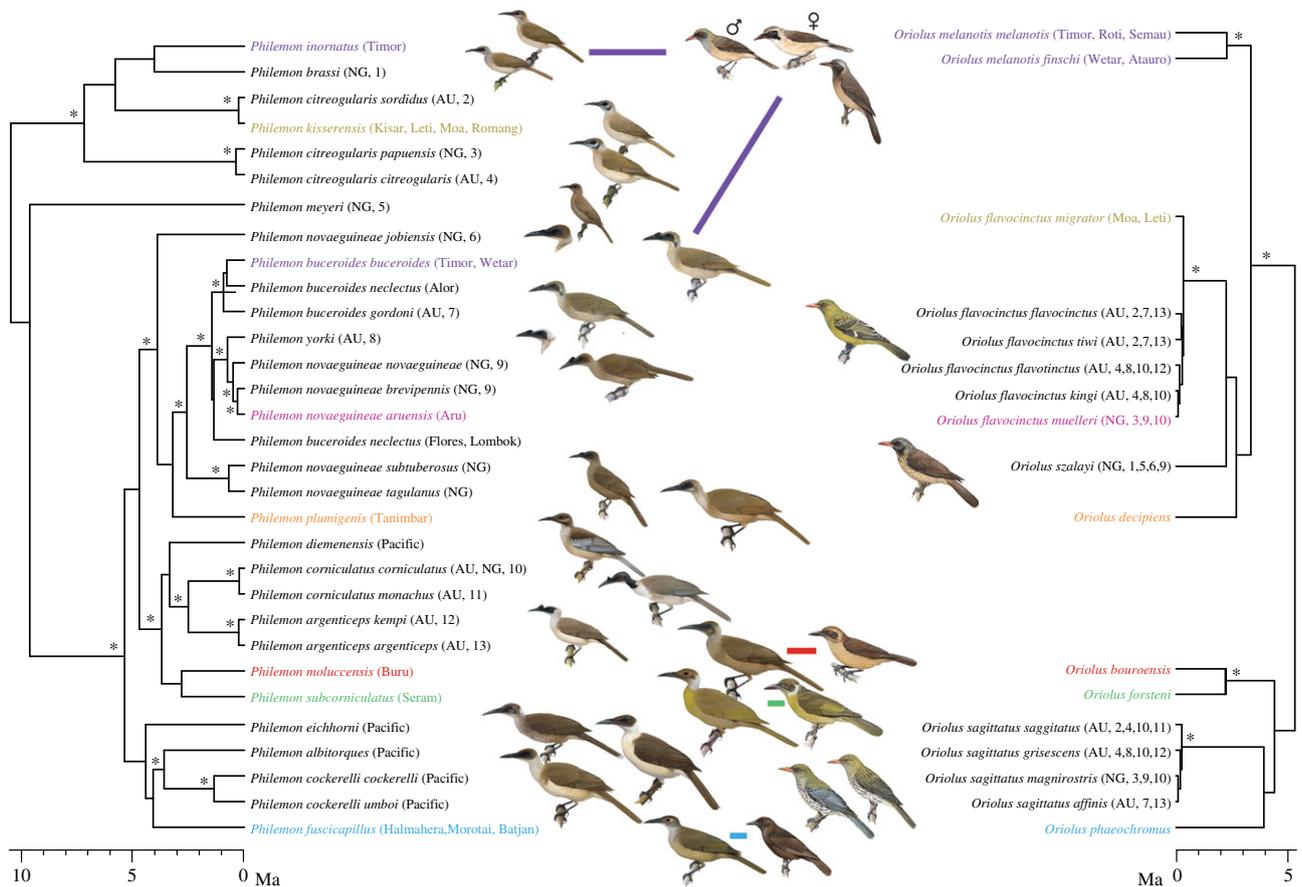


Figure 1. Distribution of coexisting friarbirds and brown orioles with the phylogeny of brown orioles oriented to match the phylogeny of friarbirds (see also electronic supplementary material, figures S3–S5 for additional phylogenetic information). Species names are coloured according to island distributions. To the right of taxon names are indicated distributions (Au, Australia; NG, New Guinea) followed by a number which indicates coexistence. For example, *Philemon brassi* (NG, 1) occurs in New Guinea and is sympatric with *Oriolus szalayi* (NG, 1,5,6,9). Timescales (in million years) are indicated below the phylogenies. Illustrations from *Handbook of the Birds of the World* [35]. Asterisks at nodes indicate posterior probabilities of 0.99–1.00.

While colonization of Wallacea by brown orioles may be the result of a single dispersal event with back-colonization to Australo-Papua, the ancestral area reconstruction analysis suggests that friarbirds colonized both the Pacific and the Wallacean archipelagos multiple times (figure 1). The dating analysis suggests that friarbirds originated 9.9 Ma (95% HPD = 8.3–11.5 Ma), whereas brown orioles originated 5.0 Ma (95% HPD = 4.2–5.9 Ma). Despite the difference in time of origin, most friarbirds colonized Wallacea and the Pacific within the last 5 Myr.

To test for the possible coevolutionary radiation between brown orioles and friarbirds, we evaluated the null hypothesis that events of speciation of coexisting friarbirds and brown orioles have taken place independently of each other. The time of speciation among all friarbird–oriole pairs was evaluated against the association from 500 randomly assigned matches of species. The timing of co-speciation among coexisting lineages was not different from the co-speciation of randomly assigned species pairs (ParaFitGlobal = 120 580.7, $p = 0.235$). Thus, there is no evidence of co-speciation among coexisting friarbirds and orioles.

(c) Colour similarity between friarbirds and orioles

Across all sympatric oriole–friarbird pairs, both size disparity and time of co-occurrence separately correlated with better mimicry across regions (table 1 and electronic supplementary material, S4 and S5). Colour contrast was lower for pairs that

had coexisted longer and for pairs where friarbirds were relatively larger than orioles. In addition, we found a significant positive interaction between both variables (table 1 and electronic supplementary material, S4 and S5) indicating that the effects of time and size together are not completely additive. Indeed, the poorest cases of mimicry were found in species pairs that had short coexistence times and where orioles were nearly as large as friarbirds (figure 3). These effects could explain why plumage colour resemblance between orioles and friarbirds is most marked in the Wallacean islands and in New Guinea compared with the Australian mainland (figure 2a, $F_{2,30} = 8.79$, $p < 0.001$). Both size differences ($F_{2,27} = 4.81$, $p = 0.016$) and coexistence times ($F_{2,30} = 7.9$, $p = 0.001$) vary between regions being lowest in Australia (figure 3). Thus, it appears that better mimicry in Wallacea and New Guinea can be explained largely by the combination of co-occurrence times and size differences.

Phylogenetic generalized-linear models confirm the effects of size differences and coexistence time presented above. At the taxon level, ($n = 14$) brown orioles that have lower colour contrast against sympatric friarbirds are those that have coexisted with relatively larger friarbirds for longer (table 2 and electronic supplementary material, S6 and S7, figures 2 and 3). Finally, orioles tend to resemble sympatric friarbirds more than allopatric ones, but this difference is not significant (phylogenetic paired t -test, mean paired colour contrast [sympatric–allopatric] = -2.04 , s.e. = 1.29, $t = -1.58$, $p = 0.14$, $\lambda = 0.66$).

Table 1. Results from linear models assessing the effects of coexistence time and size difference between sympatric oriole–friarbird pairs and their interaction on colour differences between orioles and friarbirds. All sympatric oriole–friarbird pairs are included as independent data points in these analyses. Sample size: 30 oriole–friarbird pairs for the interaction and size difference models and 33 pairs for the coexistence time model. Sample size difference owing to missing morphological data on *Philemon corniculatus comicalatus*.

	interaction model				coexistence time model				size difference model			
	estimate	s.e.	t	p	estimate	s.e.	t	p	estimate	s.e.	t	p
intercept	−8.90	5.99	−1.49	0.149	9.72	0.75	12.95	0.000	−4.81	4.881	−0.985	0.3329
coexistence time (millions of years)	6.82	3.94	1.73	0.095	−1.68	0.60	−2.79	0.009	—	—	—	—
relative size difference (tarsus length)	23.53	7.48	3.14	0.004	—	—	—	—	16.617	6.153	2.701	0.0116
coexistence time × size difference	−10.99	5.24	−2.10	0.046	—	—	—	—	—	—	—	—
	adjusted $R^2 = 0.36$				adjusted $R^2 = 0.17$				adjusted $R^2 = 0.17$			

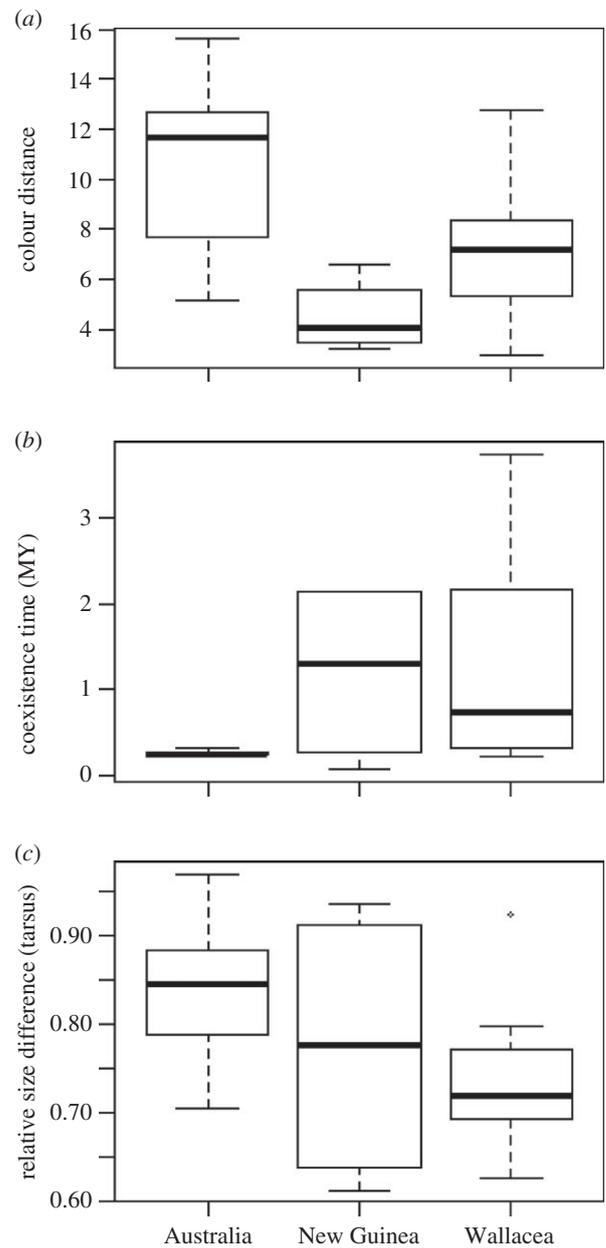


Figure 2. Colour contrast between orioles and sympatric friarbirds varies across the study region (a) as does coexistence time (b) and size difference measured as the ratio between oriole and friarbird tarsus length (c).

4. Discussion

Recently, Prum [3,40] summarized the current knowledge of ISDM in birds and set forth predictions of the ISDM model. First, ‘Visual deception should be physiologically plausible at ecologically relevant visual distances between individuals’. This is certainly the case for this study system as both the models and mimics are medium-sized passerine birds that often feed (and compete for resources) in the same fruiting trees [7].

Second, ‘Model species are larger in body mass than mimic species, and socially dominant over them’. Our morphological data demonstrate that members of *Philemon* and *Oriolus* overlap in size. However, while comparing coexisting orioles and friarbirds, it is clear that there are notable size differences between the models (larger) and the mimics, particularly in the Indonesian islands. Diamond [7] suggested that a larger difference in size between co-occurring friarbirds and brown orioles led to better mimicry. He hypothesized

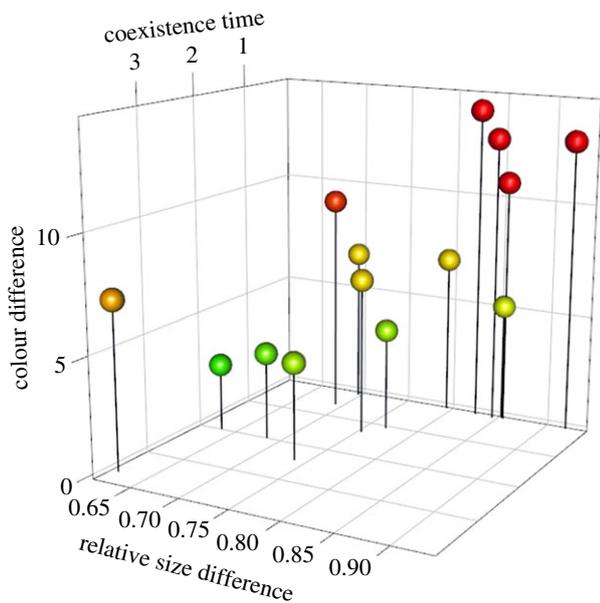


Figure 3. Average coexistence time and relative size difference correlate with the level of colour contrast between orioles and coexisting friarbirds. Red colours depict high and green colours low values of colour contrast. (Online version in colour.)

that if mimicry had evolved because it enabled orioles to feed alongside aggressive friarbirds, there would be a stronger selection on small orioles to mimic friarbirds as they would be more vulnerable to attacks. Based on a large-scale survey, Prum [3] found that linear dimensions of mimics are on average 82% of the model, which is in good agreement with our study (the tarsus length of orioles was on average 76% of that of sympatric friarbirds, $n = 14$). However, the relative size differences between the model and the mimic varied greatly within the study system (the linear dimensions of mimics ranged between 62% and 92%), and this variation was correlated with colour contrast (figures 2 and 3). Orioles that are substantially smaller than co-occurring friarbirds show lower levels of colour contrast to the model and are therefore better mimics.

Third, 'Model and mimic species are not closest relatives, and are each more closely related to other species that differ in their appearance'. It is well established that friarbirds and brown orioles belong to different clades (Meliphagidae and Oriolidae) that are well separated in the passerine tree [41]. Our phylogenetic analyses of the two groups show that the origin of friarbirds dates back to the Miocene (9.9 Ma) with the majority of taxa having evolved within the last 5 Myr. This probably reflects the emergence of an extensive archipelago to the west of New Guinea [42], which was colonized multiple times by friarbirds (figure 1 and electronic supplementary material, figure S3). Brown orioles originated later (5.0 Ma), and the number of colonizations of the Wallacean archipelagos remains unclear. While the biogeographic origins of the clades are ambiguous, the results suggest that they both colonized and diversified within Wallacea at roughly the same time during the Late Miocene and the Early Pliocene. Consequently, some friarbirds and brown orioles may have coexisted for millions of years on these islands. Our results show that friarbirds and brown orioles do not represent a case of co-speciation but that the sequential order of island colonization across the Wallacean islands

Table 2. Results from phylogenetic linear models assessing the effects of coexistence time and size difference between sympatric oriole–friarbird pairs and their interaction on colour differences between orioles and friarbirds. Phylogenetic relatedness was accounted for by using the phylogeny of orioles depicted in figure 1. For orioles that are sympatric with more than one species of friarbird, values of colour distance, coexistence time and size difference were averaged prior to the analysis so that each oriole taxon entered the analysis once. Sample size: 14 oriole taxa.

	interaction model				coexistence time model				size difference model			
	estimate	s.e.	t	p	estimate	s.e.	t	p	estimate	s.e.	t	p
intercept	-13.16	9.21	-1.43	0.184	8.97	1.62	5.55	<0.001	-8.72	7.01	-1.24	0.238
coexistence time (millions of years)	15.09	7.02	2.15	0.057	-1.50	0.82	-1.82	0.093	—	—	—	—
relative size difference (tarsus length)	28.08	11.31	2.48	0.032	—	—	—	—	20.64	9.29	2.22	0.046
coexistence time \times size difference	-22.94	10.25	-2.24	0.049	—	—	—	—	—	—	—	—
	adjusted $R^2 = 0.39$				adjusted $R^2 = 0.15$				adjusted $R^2 = 0.23$			
	lambda = 0.53				lambda = 0.30				lambda = 0.54			

took place in different ways for the two groups. However, there is one plausible instance of co-speciation among species on the neighbouring Moluccan islands of Buru (*Philemon moluccensis* mimicked by *Oriolus boroensis*) and Seram (*Philemon subcorniculatus* mimicked by *Oriolus forsteni*; figure 1).

Finally, ‘SDM can create a coevolutionary arms race in visual appearance. If geographic isolation or speciation occurs subsequent to the origin of mimicry, independent populations of models and mimics may produce coevolutionary radiation in visual appearance among clades’. Diamond [7] pointed out several convincing reasons that brown orioles mimic friarbirds and not vice versa. However, the mimicking brown orioles are not a monophyletic assemblage of species (figure 1 and electronic supplementary material, figure S3). Our analyses suggest that different lineages of brown orioles currently present in the Moluccan islands (*O. phaeochromus*, *O. boroensis* and *O. forsteni*) and in the lesser Sunda islands (*O. decipiens* and *O. melanotis*) have evolved improved mimicry compared with their relatives in Australia. It is uncertain if the brown oriole clade adapted to mimic friarbirds early on or if being brown simply provided a selective advantage that could be further honed once brown orioles came into contact with friarbirds in depauperate island ecosystems. Following Diamond’s [7] observations, we found a negative relationship between levels of plumage divergence and size divergence, thereby confirming that the closest plumage similarity (i.e. the strongest mimicry) is found in the coexisting species pairs that differ most in size. In addition, we found that the duration of coexistence between friarbirds and orioles also affected the degree of mimicry. Oriole–friarbird pairs that have presumably coexisted for longer times had lower levels of colour contrast (figures 2*b* and 3). Taken together, these results suggest that both the strength of selection to avoid aggression, which should be more intense the larger the size difference, and the opportunity for phenotypic change to happen afforded by longer periods of coexistence, have shaped the evolution of mimicry in brown orioles.

5. Conclusion

We present a detailed analysis of a classic example of visual mimicry in birds in Australo-Papua and the surrounding archipelagos, using nearly complete dated molecular subspecies-level phylogenies, and drawing on several lines of evidence to determine how brown orioles (the mimics) evolved in relation to friarbirds (the model). Consistent with the mimicry hypothesis, our analyses show that friarbirds evolved before

brown orioles and that they speciated and dispersed largely independently of each other in Australo-Papua and the surrounding archipelagos. In the depauperate island environments, improved mimicry probably facilitated the persistence of brown orioles. Our data also show that orioles tend to better match the colour of sympatric friarbirds than allopatric friarbirds. Finally, a longer history of co-occurrence and a larger size difference between model and mimic lead to better mimicry, ultimately allowing for the existence of both friarbirds and orioles on Wallacean islands.

Data accessibility. Genetic sequences are uploaded on GenBank (KX272488–KX272597, electronic supplementary material, table S1). Plumage coloration data are available from the electronic supplementary material.

Authors’ contributions. K.A.J., G.S. and M.I. conceived the study and carried out the sequencing. K.A.J. collected the morphological data and K.D. collected the plumage coloration data. K.A.J. and K.D. performed the analyses and interpreted the analyses. K.A.J. wrote the manuscript with input from all other authors.

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