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Integumentary Colour Allocation in the Stork Family (*Ciconiidae*) Reveals Short-Range Visual Cues for Species Recognition

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Simple Summary: The *Ciconiidae* family includes 19 extant species distributed in both the Old and the New World. While all species are similar in morphotype, with dominant black or white plumage colouration, storks may also display some highly coloured areas in small patches of the integument, including bill, legs, and the head. We have tested the conservatism of colour characters in different parts of the body, aiming at detecting highly and lowly conserved characters. Non-conserved coloured areas are located in frontal zones but cover a low proportion of the entire body and are only visible at close range. These results provide further support to the species recognition hypothesis to explain colour patch allocation in closely related bird species with sympatric distributions.

Abstract: The family *Ciconiidae* comprises 19 extant species which are highly social when nesting and foraging. All species share similar morphotypes, with long necks, a bill, and legs, and are mostly coloured in the achromatic spectrum (white, black, black, and white, or shades of grey). Storks may have, however, brightly coloured integumentary areas in, for instance, the bill, legs, or the eyes. These chromatic patches are small in surface compared with the whole body. We have analyzed the conservatism degree of colouration in 10 body areas along an all-species stork phylogeny derived from BirdTRee using Geiger models. We obtained low conservatism in frontal areas (head and neck), contrasting with a high conservatism in the rest of the body. The frontal areas tend to concentrate the chromatic spectrum whereas the rear areas, much larger in surface, are basically achromatic. These results lead us to suggest that the divergent evolution of the colouration of frontal areas is related to species recognition through visual cue assessment in the short-range, when storks form mixed-species flocks in foraging or resting areas.

Keywords: wading birds; hybridization; visual signals; assortative mating; character displacement

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Citation: Rodríguez-Rodríguez, E.J.; Negro, J.J. Integumentary Colour Allocation in the Stork Family (*Ciconiidae*) Reveals Short-Range Visual Cues for Species Recognition. *Birds* **2021**, *2*, 138–146. https://doi.org/10.3390/birds2010010

Academic Editor: Jukka Jokimäki

Received: 4 February 2021
Accepted: 12 March 2021
Published: 17 March 2021

1. Introduction

The storks (*Ciconiidae*) are large wading birds inhabiting tropical and temperate areas of the world, with the majority of the 19 extant species of the family inhabiting Africa and southern Asia [1]. Only three Palearctic species perform long distance migrations, leaving temperate areas of Eurasia to winter in sub-Saharan Africa (i.e., European White Stork *Ciconia ciconia* and Black Stork *Ciconia nigra*), or from northern east Asia to southern Asia (Oriental White Stork *Ciconia boyciana*). They are generally social nesters and foragers, and sometimes form mixed species colonies, either with other stork species and/or with other wading birds such as spoonbills, herons or ibises [2].

All storks share a similar morphology and phenotype: long legs and necks, large and strong beaks, and body plumage colouration ranging the whole achromatic spectrum. As such, they comprise almost all-white (e.g., the Wood Stork *Mycteria americana*), black and white (e.g., the European White Stork), slate-grey (e.g., Marabou *Leptoptilos crumenifer*), and all-black species (e.g., the African Openbill *Anastomus lamelligerus*). With such a description, it may seem that storks are dull-coloured and rather uniform. However, the stork family displays an impressive array of colour-producing mechanisms in both feathers and bare parts: the dark plumage colouration is due to melanins, but some species produce iridescence, a partially structural and partially pigmentary mechanism [3], while others do not. Sheen feathers [4], a specialized type of feather structure that may enhance long-distance communication, is also present in several species. Beak and leg colouration also varies, being bright red due to carotenoids in a number of species, or entirely black due to melanins in others. Eye colour also shows great variation, with no less than five distinct iris colours (see below) present in the family. Pigments involved in iris colouration include melanins, carotenoids and pteridins [5,6]. In fact, even though there are no stork species sexually dichromatic in relation to plumage colouration, the two species of *Ephippiorhynchus* are sexually dichromatic for just iris colouration [6]. Many stork species have bare portions of the head, or even the whole head and neck. Sometimes the exposed skin is coloured, either by melanin, carotenoids, or by the haemoglobin in circulating blood through skin vessels [7]. The metabolic pathways for each of these pigments differs, as well as their signaling potential. Melanins and haemoglobin are endogenously synthesized by the birds, whereas carotenoids are necessarily ingested from the diet [8]. Carotenoids may be linked to foraging efficiency and also to body condition and thus individual quality [9]. Therefore, carotenoid-dependent colouration is more often related to sexual selection than melanin-dependent colouration, which in turn is largely responsible for composing cryptic patterns [10,11].

By being of a larger size than most birds, and having stout bills, storks have no major predators [2]. Their colouration is not particularly cryptic, as plumage patches are solidly coloured and unpatterned, except for a few cases such as the wing covert feathers of the *Mycteria* species [10]. It is possible that their overall colouration is more determined by thermoregulation needs [7], feather resistance [12], or intraspecific communication than by vulnerability to predation. Sexual dichromatism is practically non-existent, although juveniles in most species are drabber in colouration compared to the definitive adult plumage. In this respect, the storks resemble gulls among Charadriifroms, and diurnal raptors among Accipitriforms and Falconiforms, where juveniles tend to be dull coloured and have less contrasting colouration than adults, which tend not to be sexually dichromatic [13]. The role of sexual selection in the evolution of colouration in all these predatory species is possibly less intense than in other avian groups with sexually dichromatic species, and with mating systems including polygyny (i.e., lekking species, [14]). Nonetheless, it is intriguing to determine how colour is partitioned across the stork radiation, and which is its diagnostic value for species recognition in sympatric taxa [15].

The extant stork species are grouped into two major clades (according to Slikas [16], and to our own phylogeny, see results). One clade includes four genera (*Jabiru*, *Ephippiorhynchus, Anastomus*, and *Mycteria*) with nine species, and the other two genera (*Ciconia* and *Leptoptilus*) with 10 species. Our objective was to assess how colour variation is partitioned between and within clades. Additionally, we wanted to determine which are the body parts with tend to vary the most in colouration. Last, we aimed to assess whether the 'species isolation hypothesis', traditionally invoked to explain interspecific colour variation in incipient bird species [17,18], may be supported in the case of the stork radiation. This hypothesis posits that a range of mating signals, including acoustic, olfactory and visual cues (e.g., [18]) facilitate species recognition and serve to avoid maladaptive hybridization, as first suggested by Wallace [19], and later expanded by Dale [20]. Martin et al. [21] have recently provided support for highest colour divergence in closely related species at intermediate levels of breeding range-sympatry using 246 bird species belonging to 39 species with a worldwide distribution.

Storks are an ideal group of species to test the visual component of this hypothesis relying on intraspecific communication because most species coincide with others in sympatry, and they display a wide colour palette considering all body parts, yet the species in the group maintain a high uniformity in general morphotype, size, and foraging substrate.

2. Material and Methods

2.1. Species and Phenotypic Variables

We have investigated the colouration of all 19 recognized extant species in the family *Ciconiidae* (we have not included the African Woolly-necked Stork *Ciconia episcopus microscelis*, considered as a full species by del Hoyo [1]). For analysis, we have considered 10 body parts known to vary in colouration, and widely varying in extent (see Figure 1): bill, head, facial skin, iris, neck, ventral area, dorsum, remiges, tail and wing covert feathers. We have searched pictures of every species on the internet [22] and have recorded the hue and possible colour-producing mechanism. Assigned colour using photographs was double checked with colour plates in Del Hoyo [1]. Comparative studies dealing with bird colouration and based on book plates are commonplace [4], as human vision provides a valid proxy for assessing avian colouration [23,24]. For feather tracts, we have distinguished white (absence of pigment), black (melanin-based), iridescence (structure and melanin), gray (melanin-based) and sheen (structure and melanin). For podotheca (legs) and ramphoteca (bill), we have assumed that red and orange is due to carotenoids [25], and black is due to the presence of melanin. Bare skin may be coloured due to carotenoids (as with the orange in the neck of the greater adjutant), to melanins or to hemoglobin if (as with the pinkish marabu's neck or the red at the base of the neck in the Jabiru *Jabiru mycteria*). In the case of iris colouration, different pigments may be involved [6].

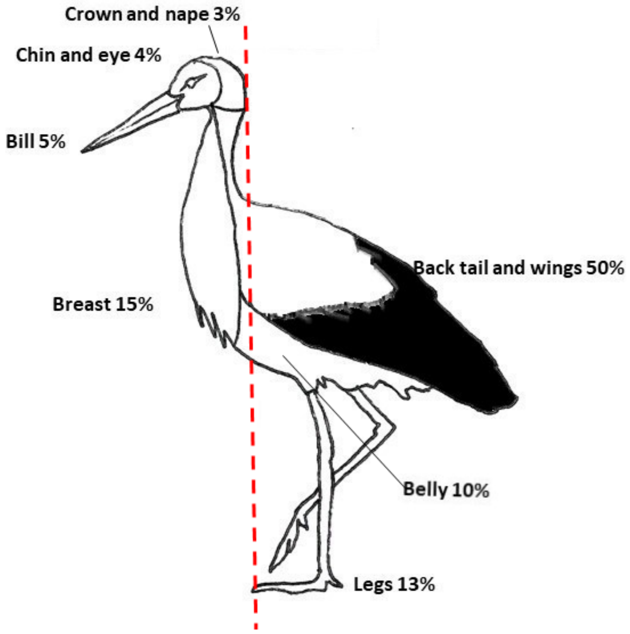

Figure 1. Regions of the stork body scored for colouration. The percentage of the surface of each region has been averaged following Yezerinac and Weatherhead [26]. The dotted red line separates frontal from rear areas of the body.

2.2. Phylogeny Data

To construct a phylogeny for the stork family comprising all species (a previous one was incomplete [16]), we obtained 100 probable phylogenies with branch lengths expressed as proportions of nucleotide substitutions using the phylogeny subsets tool in www.birdtree.org (accessed on 4 February 2021) [27], and then obtained the least-squares consensus phylogenetic tree using the R package Phytools [28].

2.3. Conservatism Measurements

As recommended by Münkemüller et al. [29], Geiger models, based on maximum likelihood, were constructed to test the conservatism of characters in relation with phylogeny, with the ER (equal rate transitions) model being the better fitted. Other models tested were SYM (Symmetric transitions are equal) and ARD (all rated different model). Models were fitted using different Bayesian methods included in the R Geiger package 2.0 [30]. These methods include the accommodating uncertainty in trait evolution using R (AUTEUR) following Eastman et al. [31], including reversible jump Markov chain Monte Carlo machinery [32] to test multivariate models of various complexities.

Body areas were classified by conservatism importance following Münkemüller et al. [29]: log-L ≤ -30 low; $-30 <$ log-L ≤ -20 medium; $-20 <$ log-L ≤ -10 high; log-L > -10 very high. The percentage of body area represented in each category of conservatism importance was calculated using Figure 1 (based in Yezarinac and Weatherhead [26], and measured using ImageJ V.2, [33]).

3. Results

The visible colouration of each character for every species is represented in Figure 2 (bill, head, iris, neck and facial skin) and Figure 3 (ventral, remiges, dorsum, tail, and legs) related with the stork phylogeny. In the first group of characters (frontal), we found a total of eight colour possibilities (and the iridescence characteristic), while in the second group we found a total of four colours plus the iridescence possibility.

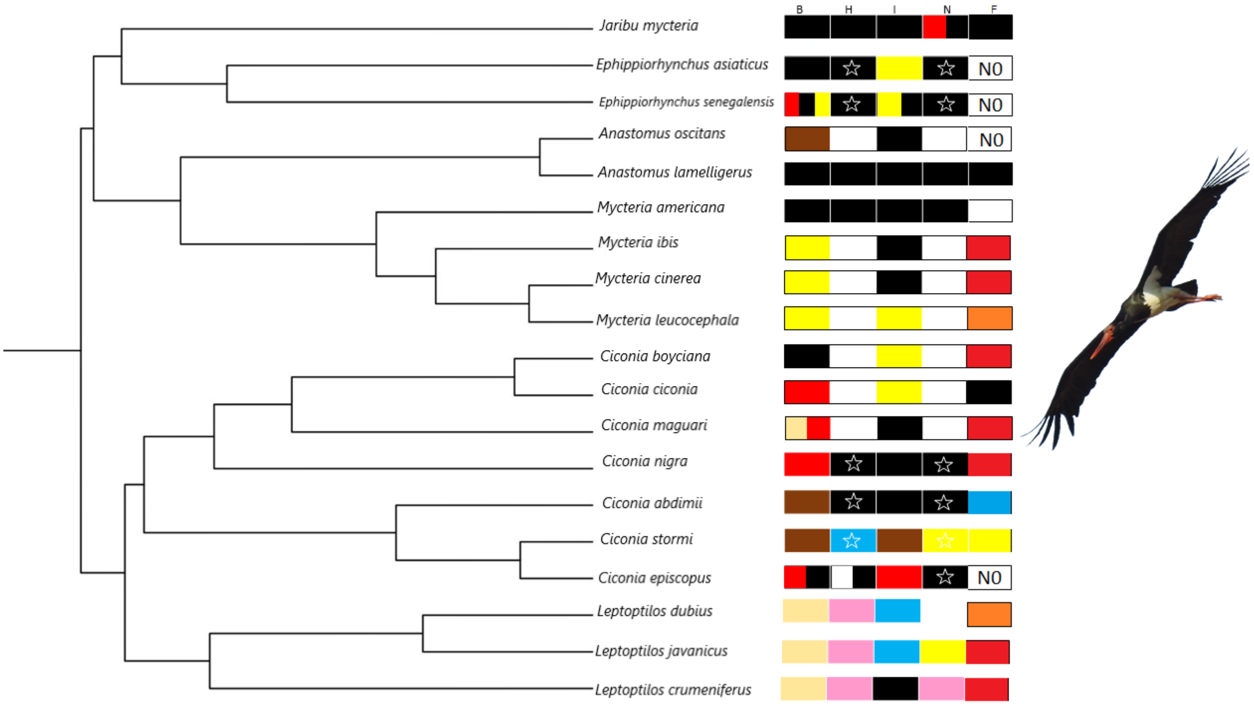

Figure 2. Stork phylogeny with colour status of frontal characters. Bill (B), head (H), iris (I), neck (N) and facial skin (F). Stars indicate iridescence. Colours used mimic the observed ones for each body region and include both achromatic (black and white) and chromatic variants (red, yellow, pink, blue, brown and orange). "No" in facial skin means that this species has no exposed skin in the face because is fully covered by feathers. Several colours for a given area in the same species indicates that those same colours concur there.

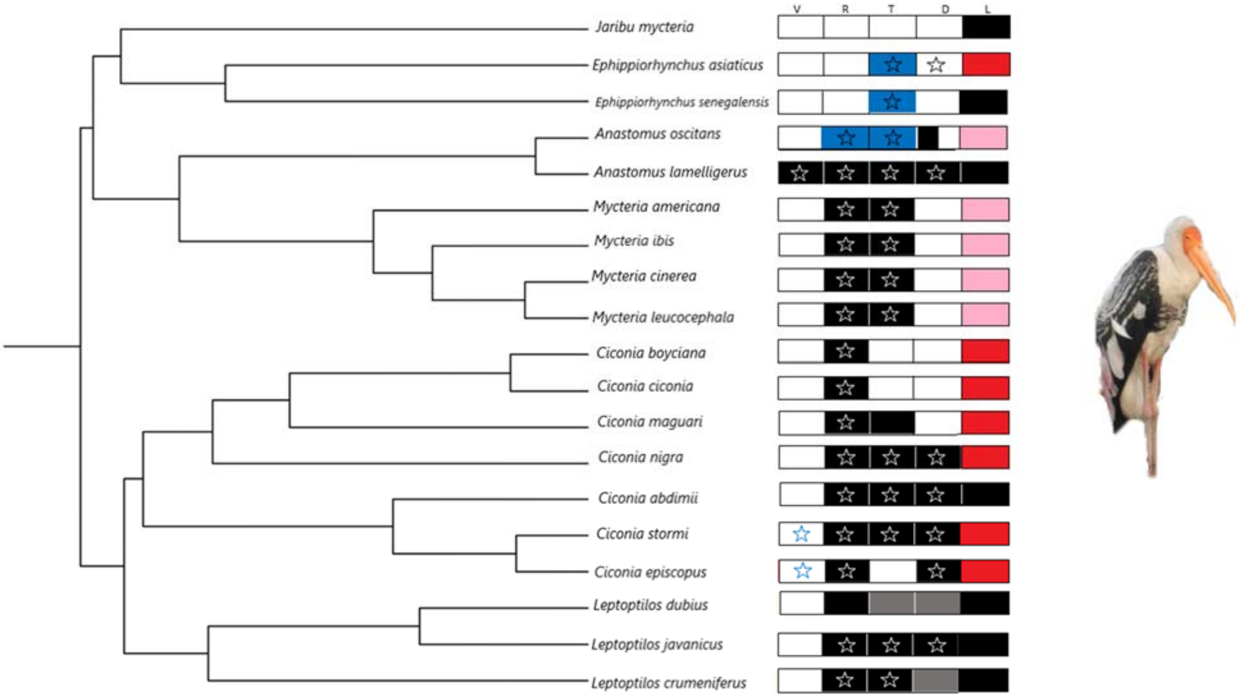

Figure 3. Stork phylogeny with colour status of non- frontal characters. Ventral (V), remiges (R), tail (D), dorsum (D) and legs (L). Stars indicate iridescence. Colours are mostly in the achromatic scale (i.e., back, white, gray and blue), except in the legs, where carotenoids are often displayed. The dorsal area of *Anastomus oscitans* is coloured both black and white, as recorded in the figure.

GEIGER-fitted comparative models of discrete data (ER model) for each studied character provide the highest log-likelihood absolute values for bill, face, neck and head; and the lowest values in ventral, remiges, legs and dorsum (see Table 1). Following Münkemüller et al. [29] classification, 12% of the body (i.e., bill, facial skin, and neck) presents a low conservatism importance, 8% medium conservatism (i.e., iris and head), a 63% high conservatism (i.e., remiges, tail, dorsum, and legs), and 17% very high conservatism (ventral) (see Table 2). Thus, only 12% of the total body area presents the majority of divergence in colour within *Ciconiidae*.

Table 1. GEIGER-fitted comparative models of discrete data (ER model) for each studied character. Log-likelihood, AIC and corrected AIC are provided.

Area.	Log-Likelihood	AIC	AICc
Bill	−40.571838	85.143677	85.943677
Legs	−16.961067	35.922135	66.753341
Facial	−32.251670	66.503341	66.753341
Iris	−24.953299	51.906597	52.156597
Ventral	−4.838572	11.677143	11.927143
Dorsum	−16.448905	34.897810	35.147810
Remiges	−15.936578	33.873156	34.123156
Tail	−19.509732	41.019464	41.269464
Neck	−32.956012	−32.956012	68.162024
Head	−29.908035	−29.908035	62.066070

Table 2. Body areas by conservatism importance classified based on log-likelihood: log-L $\leq -$ 30 low; $-30 <$ log-L ≤ -20 medium; $-20 <$ log-L ≤ -10 high; log-L > -10 very high. Percentage of body areas also provided. Measurements taken using Image J [33].

Degree of Conservatism	Body Regions	% of Body Surface
Low	Bill, facial skin, neck	12%
Medium	Iris, head	8%
High	Remiges, tail, dorsum, legs	63%
Very high	ventral	17%

4. Discussion

The reasons underlying different colouration in birds has been hotly debated for decades [17,34,35], although their variation may only be a reflection of the enormous colour space, or colour gamut, achieved by Class Aves [36] compared to the other land vertebrates, and mammals in particular [37,38]. As an example of within-genus colour diversity, the *Monarcha* species in the geographically restricted Solomon Islands differ most dramatically in plumage colouration than in any other morphological character [39,40]. This bird radiation is a very recent one, with all forms (classified as either subspecies, allospecies or full species) emerging in the last 500,000 years [40]. Other island radiations provide similar examples of high colour diversity, such as the Hawaiian honeycreepers (Fringillidae), including both drab and colourful species [41]. Contrary to other morphological traits, such as beak size or tarsus length, colouration is a poor indicator of dietary niche, foraging substrate or foraging behavior [42]. In fact, colouration diversity is considered to rapidly emerge due to character displacement to avoid maladaptive hybridization [17,43]. In fact, distinctive colour differences between incipient species have been linked to a single amino substitution in the Melanocortin-1 Receptor [18]. Therefore, a point mutation may contribute to speciation. The ‘species isolation hypothesis’ implies that colouration is a very flexible trait rather decoupled from ecological pressures and linked, however, to intraspecific communication, sexual selection and, in turn, species recognition [44].

The conservatism of a phenotypic character can be defined as its maintenance in a group of species or phylogenetically related lineages. Conservatism is maintained by a selective pressure, related to niche, over a functional character [45]. Regarding colour of the dorsal area and belly, we suggest that most of its surface accomplish an adaptive function, and this is the reason for a selective maintenance of overall colouration and thus, conservatism. For instance, remiges and rectrices may be coloured black, even in species with overall white colouration, such as the white stork, because melanin is known to provide structural resistance to mechanical breakage and abrasive wear [46,47]. On the other hand, the colour of smaller body regions may be less important for functional adaptation and could diverge due to the mechanism of character displacement driven by the need for species recognition.

The latter could be defined as a measurable difference in behavioral responses toward conspecifics as compared to heterospecifics [48]. This is highly relevant because in many cases mating with heterospecifics may result in low-fitness or inviable offspring. Although in few cases it has generated adaptive hybrids [48], the mating among heterospecifics usually results in maladaptive hybridization [49].

We have studied an avian family, the *Ciconiidae*, in which all extant members have kept a recognizable and uniform morphotype (long legs, necks and beaks), as well as similar foraging substrates (i.e., wetlands and open grasslands). By assigning colouration to 10 body parts in each species under investigation, we aimed to determine not only how these species can be described in terms of colouration pattern, but also whether some body parts tend to vary more often than others.

Our results are consistent with a species recognition explanation for the concentration of colour divergence in head and neck of storks. This applies to the two major clades as well as pairs of sister species that have diverged quite recently (e.g., European White Stork and Oriental White Stork, or Woolly-necked stork and Storm’s stork). The colour patches involved, that should be evaluated at a short distance (e.g., iris colour differences), seem to be aimed at individuals tolerated in close proximity, and these traits could facilitate the avoidance of maladaptive traits, and thus, promote species maintenance and divergence. The cues provided by colourful patches may also facilitate plain species recognition in highly social taxa that often form interspecific foraging or resting aggregations [50]. It is logical to think that the beginning of these colour differences arises from incipient divergence among lineages produced by reproductive isolation generated by barriers or differences in niche use [51]. Then, recognition among individuals of different lines and assortative mating increases the divergence in, for instance, facial and neck colouration, whereas in other body areas this is not as evident and possibly more conservative due to a maintenance by functional selection [52].

The 'species isolation hypothesis' should apply to species at high risk of finding the wrong mate because they easily encounter both conspecifics and members of other species with similar phenotypes. The majority of the storks are highly social and tend to forage sympatrically with other stork species or other large wading birds, exhibit delayed plumage maturation and delayed reproduction [53]. In this regard, it may be advantageous for an individual, whether sexually mature or not, to recognize not only compatible mates, but also conspecifics and their different ages to decide, for instance, to join a flock about to move among foraging patches and/or roosting sites, or even departing on migration [54].

Author Contributions: E.J.R.-R.: analysed the data, prepared the figures and helped in manuscript writing. J.J.N.: conceived the research and wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: No ethical issues involved.

Data Availability Statement: Color data used in this research are available within the paper in Figures 1 and 2. Sequence data for phylogeny available at BirdTree.org.

Acknowledgments: We are very thankful to two anonymous reviewers for their constructive comments on an early version of the manuscript. This work has been accomplished without any financial support.

Conflicts of Interest: The authors declare no conflict of interest.

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