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The evolution of courtship displays in Galliformes

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ABSTRACT

Species in Galliformes have elaborate ritual courtship displays, often including strutting, fluffing of tail or head feathers, and vocal sounds that serve as excellent examples of sexual selection. According to the male orientation to the female while either posturing or moving, these courtship displays of gallinaceous species can be classified into three categories: 1) 'frontal displays', 2) 'lateral displays', and 3) 'both frontal and lateral displays'. Questions regarding which category of displays is the ancestral state and the evolutionary history of courtship displays in Galliformes remain unanswered. We collected and classified 131 species in terms of their courtship displays into the three categories listed above and carried out a large-scale comparative analysis to reveal the evolutionary trajectory of this trait. We found that the ancestral state of courtship displays of Galliformes involves both relatively short and straightforward frontal and lateral elements (i.e., the category of 'both frontal and lateral displays'). Furthermore, ancestral trait reconstructions suggest that transitions from 'lateral displays' to 'frontal displays' occurred more frequently than the other way around (i.e., from 'frontal displays' to 'lateral displays'). In addition, some transitions occurred from 'both frontal and lateral displays' to 'lateral displays' but not from 'both frontal and lateral displays' to 'frontal displays'. Ancestral state reconstruction of courtship displays at the root of the Galliformes phylogeny supports the 'both frontal and lateral displays' first scenario. This original state then evolved towards two extremes, either 'frontal displays' or 'lateral displays', with more complicated and elaborate display components. Moreover, subsequent transitions occurred from 'lateral displays' to 'frontal displays' much more frequently than the other way around during the evolutionary history, indicating positive selection of 'frontal displays'.

1. Introduction

Courtship display – a suite of behaviours displayed by an individual to attract and eventually reproduce with an individual of the opposite sex – is an essential feature of animals, fulfilling a variety of crucial functions such as sex recognition, sexual stimulation, synchronization of mating behaviour, affecting female choice process and moderation of female aggression (Bastock, 1967; Mitoyen et al., 2019). Research efforts to investigate courtship displays in the animal kingdom have mainly focused on the visually conspicuous dances and acoustic calls of birds, especially species in Galliformes (Dinsmore, 1970; Prum, 1990; Fiske et al., 1998). According to the male orientation to the female while either posturing or moving and the male body's symmetricity during displaying, courtship displays of gallinaceous species can be classified into three categories: 1) 'frontal displays', 2) 'lateral displays', and 3) 'both frontal and lateral displays' (del Hoyo et al., 1994). Specifically, the male faces the female with spreading the wings or tail in the category of 'frontal displays', which tends to be symmetrical (Fig. 1A). On the other hand, 'lateral displays' often involve spreading wings and the tail in such an unsymmetrical way that the bird appears more significant when viewed from the side (McGowan et al., 2020, Fig. 1B). In the third category, courtship displays of these species include elements of 'both frontal and lateral displays' (del Hoyo et al., 1994).

Galliformes is an order of birds that includes turkey, chicken, quail, and other landfowl. This avian group features heavy-bodies with ground feeding and is adapted to almost any environment except for innermost deserts and perpetual ice (Tian et al., 2018; del Hoyo et al., 2020). Galliformes contains 295 species divided into five families: Megapodiidae (incubator birds like malleefowl and brush-turkeys); Cracidae (including chachalacas and curassows); Numididae (guineafowls); Odontophoridae

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Fig. 1. Typical examples of courtship displays in Galliformes. (A) A male *Tragopan caboti* conducts 'frontal displays' by flashing his colourful wing linings and inflating his decorative wattle. Photo by The Management Center of Wuyanling National Nature Reserve in Zhejiang. (B) A male *Lophura bulweri* erects and enlarges his wattles, raises and spreads his striking snow-white tail with a typical 'lateral display' (in such an unsymmetrical way that the bird appears more significant when viewed from the side). Photo by Tomasz Doroń.

(New World quails), and Phasianidae (including chicken, quail, partridges, pheasants, turkeys, peafowl (peacocks) and grouses) (del Hoyo et al., 2020). Some species in this order are economically and culturally valuable as they are domesticated for a long history for food and appeared in ancient literature and artworks (Fuller and Garson, 2000; Persons et al., 2016).

Gallinaceous species have been model organisms for studying sexual selection, with the classic system being the plumage patterns and large tail-coverts of peacock (*Pavo cristatus*). It is well known that the male peacock's sexual display is among the most spectacular in nature and consists of both a glittering train and crest plumage along with various behavioural traits (Jaiswal et al., 2021). It was, in fact, Charles Darwin's fascination with the peacock that shaped his theory of sexual selection (Darwin, 1871). Furthermore, as Darwin wrote, "What a contrast is presented between the sexes by the polygamous peacock or pheasant, and the monogamous guinea-fowl or partridge!" (Darwin, 1871), which indicates that there is an extraordinary diversity of sexual dimorphism and dimorphic behaviour across all species in Galliformes. Indeed, species in this order have elaborate ritual courtship displays – often including strutting, fluffing of tail or head feathers, and vocal sounds – that serve as excellent examples of sexual selection. However, even though some species within Galliformes have elaborate and sophisticated courtship displays, on the other hand, some species have courtship displays that are rather short and straightforward in this avian group. Therefore, this contrast (i.e., rather short and straightforward displays to extremely elaborate and sophisticated displays) offers a unique opportunity to study the evolution of courtship displays using comparative methods and further makes Galliformes an interesting group for studying mating behaviours under the theory of sexual selection. One of the key and fundamental questions regarding courtship displays remaining unknown is: which category of courtship displays is the ancestral trait, and what is the evolutionary history of courtship displays in Galliformes?

Here, we investigate the origin of courtship displays and their evolutionary history over the galliform phylogeny. With 131 gallinaceous species' courtship displays, we first classified them into three categories (i.e., 'both frontal and lateral displays', 'frontal displays', and 'lateral displays'). Then we undertook a larger-scale comparative analysis with ancestral state and transition rate analyses by phylogenetic reconstruction of this trait. Our primary aim is to summarize and complement more courtship display data in Galliformes. At the same time, we aim to reveal the ancestral state and evolution of this trait; propose potential selection drives on courtship displays in this avian group.

2. Methods

2.1. Classification of courtship displays

We assessed all 295 gallinaceous species for their courtship displays. Data on courtship displays (description notes, live videos or pictures) are from five sources that are: 1) description notes of sexual behaviour in the 'Behaviour' or 'Breeding' section; or 2) courtship display videos from the 'Multimedia' section of the species account from *Birds of the World* (del Hoyo et al., 2020); 3) courtship videos from YouTube obtained by searching with the keywords 'species name' + 'mating' or 'display' or 'breeding' or 'sexing' or 'courtship'; 4) courtship videos or pictures from other website media (e.g., Baidu, Youku) or personal communication; 5) for those species for which we cannot obtain any valuable data from the above four sources, we searched the literature on their courtship displays from Google Scholar. Birds were classified into the following three categories according to their courtship displays: 1) 'frontal displays', in this category, the male typically faces the female with spreading the wings or tail and tends to do so symmetrically (e.g., *Tragopan caboti*); 2) 'lateral displays', in contrast to 'frontal displays', displays by species in this category often involve spreading wings and the tail in such an unsymmetrical way that the bird appears more significant when viewed from the side (usually the wing close to the female is dropping and the farther wing is stretching above the body, e.g., *Polyplectron malacense*); 3) 'both frontal and lateral displays', where courtship displays in this category include both elements of frontal and lateral displays (e.g., *Acryllium vulturinum*). For those species recorded with description notes either from *Birds of the World* or the published literature, we implemented the criterion that their courtship displays were clearly identified as 'frontal displays', 'lateral displays' or 'both frontal and lateral displays' (e.g., Sichuan Partridge *Arborophila rufipectus*, from Liao and Hu (2010) stating that this species has 'lateral displays'). On the other hand, for those species with pictures or videos of courtship displays (either from *Birds of the World*, YouTube, or other websites), we implemented the criterion that the video or picture clearly showed the species' courtship displays.

After classifying courtship displays, we matched the scientific names from *Birds of the World* (del Hoyo et al., 2020) with the species names from a phylogenetic information source (www.birdtree.org, Jetz et al., 2012), which we used for further statistical analyses. By doing so, we ended up with 131 species for which we had data on their courtship displays. The 131 species included 12 species with courtship display description notes, 10 species with courtship display videos from the website of Birds of the World, 76 species with courtship videos from YouTube, six species with courtship videos or pictures from other website media or personal communication and 27 species from the literature.

2.2. Statistical analyses

All analyses were carried out within the R statistical environment (R Development Team, 2021). First, we used the 'ace' function in the R package 'ape' (Paradis and Schliep, 2019) to reconstruct ancestral states at internal nodes of the tree. Specifically, we tested three different models: 1) the 'all rates different' model ('ARD' model) to allow independent estimates for transitions to and from the three states; 2) the 'all rates equal' model ('ER' model), and 3) a model assuming symmetrical transition rates between states ("SYM" model') to estimate the ancestral state of this discrete trait (i.e., 'frontal displays', 'lateral displays' or 'both frontal and lateral displays'). We ultimately chose the best fit model using the likelihood ratio test.

Second, we used stochastic character mapping with the function 'make.simmap' in the R package 'phytools' (Revell, 2012) to estimate evolutionary transitions between three states: 'frontal displays', 'lateral displays' or 'both frontal and lateral displays'. This allowed us to estimate the number of times gallinaceous species' courtship displays evolved from a reconstructed ancestral state and transitions between the other two categories of this trait. To account for phylogenetic uncertainty, stochastic maps were generated for 100 phylogenetic trees (Jetz et al., 2012), and the results represent an average across these trees. Again, we used three models with the function (i.e., 'ARD' model, 'ER' model, and 'SYM' model) to estimate the evolutionary transitions between three states, and the likelihood ratio test was used to assess the performance of these three models.

3. Results

3.1. Phylogenetic signals of courtship displays in Galliformes

For all 131 (44% of Galliformes) species for which courtship displays were recorded from data sources, there were three species of Megapodiidae, 13 species of Cracidae, one species of Numididae, 20 species of Odontophoridae, and 94 species of Phasianidae (Table 1). Of these, 24 species (18%) had 'both frontal and lateral displays', 89 species (68%) had 'frontal displays', and 18 species (14%) had 'lateral displays' (Table 1).

There is a strong phylogenetic signal of courtship displays in this order (Fig. 2, λ close to one). In detail, all species in Cracidae had 'frontal displays'. For species in Megapodiidae and Numididae, courtship displays had either 'both frontal and lateral displays' or 'frontal displays'. For those species in Odontophoridae, most of them had 'both frontal and lateral displays', except for two species with 'lateral displays'. However, for those species in 'Phaslanidae', courtship displays had a diverse pattern: species of grouse, turkeys, peafowls, monals, and tragopans mainly had 'frontal displays'; on the other hand, species of peacock-pheasants, and some pheasants (e.g., *Chrysolophus pictus*, *Chrysolophus amherstiae* and *Gallus gallus*) had 'lateral displays' (Fig. 2).

3.2. The ancestral state of courtship displays in Galliformes

The ancestral state analysis using three models (i.e., 'ARD', 'ER', and 'SYM' models) to reconstruct the ancestral state of courtship displays showed that the 'ARD' was the best fit model (likelihood value: −55.3) compared with the 'ER' (−62.2, likelihood ratio test, $p = 0.02$) and the 'SYM' model (−61.1, likelihood ratio test, $p = 0.01$). This ancestral state reconstruction ('ARD' model') revealed that the most likely state at the root of the phylogeny was the category of 'both frontal and lateral displays' (probability of root being 'both frontal and lateral displays': 0.69, Fig. 2).

3.3. Transitions between 'frontal displays', 'lateral displays' or 'both frontal and lateral displays'

Similarly, we found that the analysis of transition rates between these three states showed that the 'ARD' model is the best fit model with the highest likelihood value (−54.6) compared with the 'ER' (−60.9, likelihood ratio test, $p = 0.03$) and 'SYM' models (−59.6, likelihood ratio test, $p = 0.02$). The analysis of transition rates between states suggests that transitions from 'frontal displays' to 'lateral displays' occurred at a much lower rate (average: 2.0) than the reverse (average: 20.5, Fig. 3). Some transitions occurred from 'both frontal and lateral displays' to 'lateral displays' (average: 4.9) but not from 'both frontal and lateral displays' to 'frontal displays' (Fig. 3). Furthermore, relatively few transitions occurred from 'frontal displays' to 'both frontal and lateral displays' (average: 3.8, Fig. 3).

4. Discussion

The courtship display is a fundamental aspect of the breeding life history of Galliformes. With 131 gallinaceous species classified for their courtship displays, including members of all families of Galliformes, we

Table 1
Summary of courtship displays of 131 species from five families in Galliformes. For each species, the family name, species name, category of courtship displays, and data source are shown. See supplemental data uploaded in this study for links to original videos, description notes, and pictures.

Family	Species	Displays	Source
Megapodiidae	*Alectura lathami*	Both	BOW video
Megapodiidae	*Leipoa ocellata*	Frontal	Youtube
Megapodiidae	*Macrocephalon maleo*	Frontal	Youtube
Cracidae	*Ortalis vetula*	Frontal	Youtube
Cracidae	*Ortalis garrula*	Frontal	Youtube
Cracidae	*Ortalis canicollis*	Frontal	Youtube
Cracidae	*Penelope albipennis*	Frontal	BOW description
Cracidae	*Penelope obscura*	Frontal	Literature
Cracidae	*Pipile pipile*	Frontal	Youtube
Cracidae	*Pipile jacutinga*	Frontal	Literature
Cracidae	*Penelopina nigra*	Frontal	Youtube
Cracidae	*Mitu salvini*	Frontal	Youtube
Cracidae	*Mitu mitu*	Frontal	Youtube
Cracidae	*Crax rubra*	Frontal	Youtube
Cracidae	*Crax alector*	Frontal	BOW description
Cracidae	*Crax fasciolata*	Frontal	BOW video
Numididae	*Acryllium vulturinum*	Both	Personal video
Odontophoridae	*Oreortyx pictus*	Lateral	BOW description
Odontophoridae	*Colinus virginianus*	Lateral	Literature
Odontophoridae	*Callipepla squamata*	Both	Literature
Odontophoridae	*Callipepla californica*	Both	BOW description
Odontophoridae	*Callipepla gambelii*	Both	BOW description
Odontophoridae	*Odontophorus gujanensis*	Both	Literature
Odontophoridae	*Odontophorus capueira*	Both	Literature
Odontophoridae	*Odontophorus melanotis*	Both	Literature
Odontophoridae	*Odontophorus atrifrons*	Both	Literature
Odontophoridae	*Odontophorus erythrops*	Both	Literature
Odontophoridae	*Odontophorus hyperythrus*	Both	Literature
Odontophoridae	*Odontophorus melanonotus*	Both	Literature
Odontophoridae	*Odontophorus speciosus*	Both	Literature
Odontophoridae	*Odontophorus dialeucos*	Both	Literature
Odontophoridae	*Odontophorus strophium*	Both	Literature
Odontophoridae	*Odontophorus columbianus*	Both	Literature
Odontophoridae	*Odontophorus leucolaemus*	Both	Literature
Odontophoridae	*Odontophorus balliviani*	Both	Literature
Odontophoridae	*Odontophorus stellatus*	Both	Literature
Odontophoridae	*Odontophorus guttatus*	Both	Literature
Phasianidae	*Arborophila rufipectus*	Lateral	Literature
Phasianidae	*Rheinardia ocellata*	Both	Youtube
Phasianidae	*Argusianus argus*	Both	Youtube/Literature
Phasianidae	*Pavo cristatus*	Frontal	BOW video
Phasianidae	*Pavo muticus*	Frontal	Youtube
Phasianidae	*Afropavo congensis*	Frontal	Youtube
Phasianidae	*Haematortyx sanguiniceps*	Frontal	Youtube
Phasianidae	*Galloperdix spadicea*	Frontal	Youtube
Phasianidae	*Galloperdix lunulata*	Frontal	Youtube
Phasianidae	*Polyplectron napoleonis*	Lateral	BOW video
Phasianidae	*Polyplectron malacense*	Lateral	BOW video
Phasianidae	*Polyplectron schleiermacheri*	Lateral	Youtube
Phasianidae	*Polyplectron germaini*	Lateral	Youtube
Phasianidae	*Polyplectron inopinatum*	Lateral	BOW video
Phasianidae	*Polyplectron chalcurum*	Lateral	Youtube
Phasianidae	*Polyplectron bicalcaratum*	Lateral	Youtube
Phasianidae	*Ammoperdix griseogularis*	Frontal	Youtube
Phasianidae	*Ammoperdix heyi*	Frontal	Youtube
Phasianidae	*Synoicus chinensis*	Both	Youtube
Phasianidae	*Coturnix japonica*	Frontal	Literature
Phasianidae	*Coturnix coturnix*	Frontal	Literature
Phasianidae	*Coturnix delegorguei*	Frontal	Literature
Phasianidae	*Coturnix coromandelica*	Frontal	Literature
Phasianidae	*Coturnix pectoralis*	Frontal	Literature
Phasianidae	*Alectoris graeca*	Frontal	Youtube
Phasianidae	*Alectoris chukar*	Frontal	Youtube
Phasianidae	*Alectoris philbyi*	Frontal	Youtube
Phasianidae	*Alectoris rufa*	Frontal	Youtube
Phasianidae	*Alectoris melanocephala*	Frontal	Youtube
Phasianidae	*Alectoris barbara*	Frontal	Youtube
Phasianidae	*Tetraogallus caucasicus*	Frontal	Youtube
Phasianidae	*Tetraogallus caspius*	Frontal	Youtube
Phasianidae	*Tetraogallus tibetanus*	Frontal	BOW video
Phasianidae	*Tetraogallus himalayensis*	Frontal	BOW description

(continued on next page)

Table 1 (*continued*)

Family	Species	Displays	Source
Phasianidae	*Pternistis natalensis*	Frontal	Youtube
Phasianidae	*Pternistis harwoodi*	Frontal	Literature
Phasianidae	*Pternistis swainsonii*	Both	BOW description
Phasianidae	*Pternistis afer*	Frontal	BOW video
Phasianidae	*Francolinus francolinus*	Frontal	Youtube
Phasianidae	*Dendroperdix sephaena*	Lateral	Youtube
Phasianidae	*Bambusicola fytchii*	Frontal	Youtube
Phasianidae	*Bambusicola thoracicus*	Frontal	Youtube
Phasianidae	*Gallus gallus*	Lateral	Youtube
Phasianidae	*Peliperdix coqui*	Lateral	Literature
Phasianidae	*Ithaginis cruentus*	Frontal	Baidu
Phasianidae	*Lophophorus impejanus*	Frontal	Youtube
Phasianidae	*Lophophorus sclateri*	Frontal	Youtube
Phasianidae	*Lophophorus lhuysii*	Frontal	Youtube
Phasianidae	*Lerwa lerwa*	Frontal	BOW description
Phasianidae	*Tetraophasis szechenyii*	Frontal	Baidu
Phasianidae	*Tragopan melanocephalus*	Frontal	Youtube
Phasianidae	*Tragopan satyra*	Frontal	Youtube
Phasianidae	*Tragopan temminckii*	Frontal	Youtube
Phasianidae	*Tragopan caboti*	Frontal	Youtube
Phasianidae	*Syrmaticus reevesii*	Lateral	Youtube/xinhuanet
Phasianidae	*Syrmaticus soemmerringii*	Frontal	Youtube
Phasianidae	*Syrmaticus mikado*	Frontal	Youtube
Phasianidae	*Syrmaticus ellioti*	Frontal	BOW video
Phasianidae	*Syrmaticus humiae*	Frontal	Youtube
Phasianidae	*Chrysolophus pictus*	Lateral	Youtube
Phasianidae	*Chrysolophus amherstiae*	Lateral	Youtube
Phasianidae	*Phasianus colchicus*	Frontal	Youtube
Phasianidae	*Crossoptilon crossoptilon*	Frontal	Baidu
Phasianidae	*Crossoptilon mantchuricum*	Frontal	Youtube
Phasianidae	*Crossoptilon auritum*	Frontal	Baidu
Phasianidae	*Lophura nycthemera*	Frontal	Youtube
Phasianidae	*Lophura leucomelanos*	Frontal	Youtube
Phasianidae	*Lophura diardi*	Frontal	Youtube
Phasianidae	*Lophura bulweri*	Lateral	Youtube
Phasianidae	*Lophura swinhoii*	Frontal	Youtube
Phasianidae	*Lophura erythrophthalma*	Lateral	Youtube
Phasianidae	*Lophura ignita*	Frontal	Youku
Phasianidae	*Perdix perdix*	Frontal	Youtube
Phasianidae	*Pucrasia macrolopha*	Frontal	BOW video
Phasianidae	*Tetrao urogalloides*	Frontal	Youtube
Phasianidae	*Tetrao urogallus*	Frontal	BOW description
Phasianidae	*Tetrao tetrix*	Frontal	Youtube
Phasianidae	*Tetrao mlokosiewiczi*	Frontal	Youtube
Phasianidae	*Tetrastes bonasia*	Frontal	Youtube
Phasianidae	*Bonasa umbellus*	Frontal	Youtube
Phasianidae	*Centrocercus urophasianus*	Frontal	Youtube
Phasianidae	*Centrocercus minimus*	Frontal	Youtube
Phasianidae	*Falcipennis falcipennis*	Frontal	Youtube
Phasianidae	*Falcipennis canadensis*	Frontal	Youtube
Phasianidae	*Lagopus lagopus*	Frontal	BOW description
Phasianidae	*Lagopus muta*	Frontal	BOW description
Phasianidae	*Lagopus leucura*	Frontal	BOW description
Phasianidae	*Dendragapus obscurus*	Frontal	Youtube
Phasianidae	*Dendragapus fuliginosus*	Frontal	Youtube
Phasianidae	*Tympanuchus phasianellus*	Frontal	Youtube
Phasianidae	*Tympanuchus cupido*	Frontal	Youtube
Phasianidae	*Tympanuchus pallidicinctus*	Frontal	Youtube
Phasianidae	*Meleagris gallopavo*	Frontal	Youtube
Phasianidae	*Meleagris ocellata*	Frontal	Youtube

provide the first view of the origin and subsequent transitions of courtship displays in this avian group. Our results revealed that courtship displays in Galliformes might have evolved from a rather short and straightforward display including both frontal and lateral elements (i.e., 'both frontal and lateral displays'). This pattern seems particularly apparent for the family of Phasianidae: species having either elaborate and sophisticated 'frontal displays' or 'lateral displays' evolved from the ancestral state of 'both frontal and lateral displays' (Fig. 2). Furthermore, our results from transition rate analysis showed that transition occurred from the state of 'lateral displays' to 'frontal displays' much more often than the other way around during the evolutionary history (average number of transitions: 20.47 vs. 2.02, Fig. 3). Here, we discuss the implications of these results and highlight some areas of particular interest and possible avenues for further research.

The analysis reconstructing ancestral states of courtship displays at the root of the phylogeny supports the 'both frontal and lateral displays' first scenario in Galliformes (Fig. 2). This analysis was based on well-established phylogenetic relationships of Galliformes (i.e., trees used in this study, Fig. 2), at least at the family level (Jetz et al., 2012). According to phylogenetic work, megapodes (Megapodiidae) are thought to have diverged first, followed by curassows (Cracidae) (Pereira and Baker, 2006). The New World quails (Odontophoridae) and guineafowl (Numididae) split off later, although the order of this is uncertain (Armstrong et al., 2001). All phylogenies suggest that the remaining taxa all belong to a single clade referred to as the Phasianidae (Kimball et al., 1999; Dyke et al., 2003), although it contains groups previously thought to be separate families such as the turkeys (Meleagridae) and grouse (Tetraonidae) (Dimcheff et al., 2002). In accordance with these phylogenetic relationships, our data showed that families at the base of Galliformes fall with the category of 'both frontal and lateral displays' (one species of Megapodiidae, 18 species of Odontophoridae, and one species of Numididae; Fig. 2). Furthermore, courtship displays from these 'basal' families are rather elemental, usually including only a few simple actions within a short period (e.g., *Alectura lathami*, *Acryllium vulturinum*) compared with much more complicated and sophisticated courtship displays from the family Phasianidae (e.g., *Tragopan caboti*, *Centrocercus urophasianus*). Therefore, we here propose that the trait of courtship displays in Galliformes originated from a state of displays with both simple frontal and lateral elements. Then, this ancestral state evolved towards two extremes, either to 'frontal displays' or 'lateral displays', but with more complicated and elaborate display components. In this process, sexual selection might be the primary driving force, which calls for future research work. Several members of the Galliformes with their courtship displays are very well studied and provide classic examples of sexual selection (Petrie et al., 1991; Petrie, 1992, 1994; Zuk et al., 1992; Mateos and Carranza, 1997; Hagelin, 2002). This makes it appealing to carry out comparative studies of these birds in terms of their life history characteristics, including mating behaviour under the framework of sexual selection.

Although our ancestral state analysis showed that the origin of courtship displays is the category of 'both frontal and lateral displays', transition rate analysis between these three states further revealed more details of the evolutionary history of this trait. Overall, the highest transition rate occurred from the state of 'lateral displays' to the state of 'frontal displays' (average transitions: 20.5, Fig. 3). However, there were much fewer transitions from the state of 'frontal displays' to the state of 'lateral displays' (average transitions: 2.0, Fig. 3). This pattern might suggest that there was direct selection towards more 'frontal displays' in Galliformes across an evolutionary time scale. Indeed, in the family of Phasianidae in which the clade diverged recently on the phylogeny (Kimball et al., 1999; Dyke et al., 2003), most species (including groups of turkeys and grouses) typically have 'frontal courtship displays'. Furthermore, 'frontal courtship displays' in this family are usually more complicated and sophisticated with longer display times. Some of these species are known as 'lekking' species (e.g., *Centrocercus urophasianus*, *Tetrao tetrix*) (Gibson et al., 1991; Baines, 1996). A 'lek' is an aggregation of males gathered to engage in competitive displays and courtship rituals, to entice visiting females who are surveying prospective partners to mate with (Fiske et al., 1998). Males of 'lekking' species are characterized by highly developed and spectacular mating displays for attracting females. With strong female mate choice (i.e., intense sperm competition under sexual selection), the variation in mating success is quite large in 'lekking' mating systems: only a small percentage of males in the whole population can mate with females, and males provide neither paternal care nor resources such as nesting or foraging sites (Mackenzie et al., 1995). In short, such elaborate courtship displays of 'lekking' species intrigued a puzzle known as the 'lekking paradox': strong sexual selection by females for specific male traits ought to erode genetic diversity by

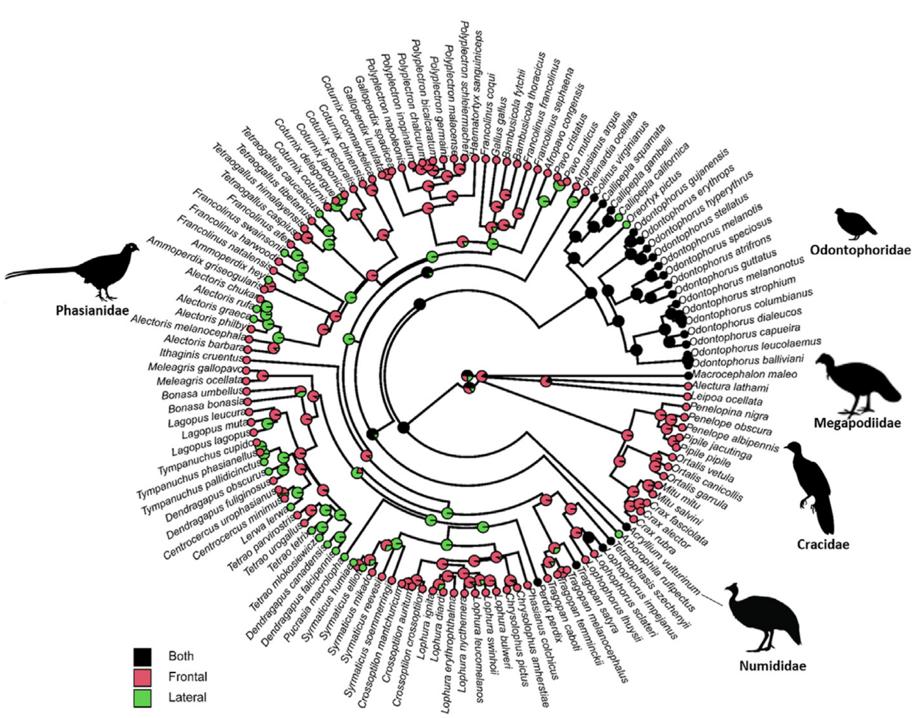

Fig. 2. Phylogenetic tree of gallinaceous species (n = 131 species) with the reconstructed ancestral state. For internal models in the tree, the posterior probability of courtship displays reconstructed using the 'ace' function from the R package 'ape' is shown. Pie colours indicate three states (i.e., 'both frontal and lateral displays', 'frontal displays', and 'lateral displays'. Small dots (with three colours) at each tip of the tree indicate three categories of courtship displays of species. Silhouettes (retrieved from www.phylopic.org) represent five gallinaceous families.

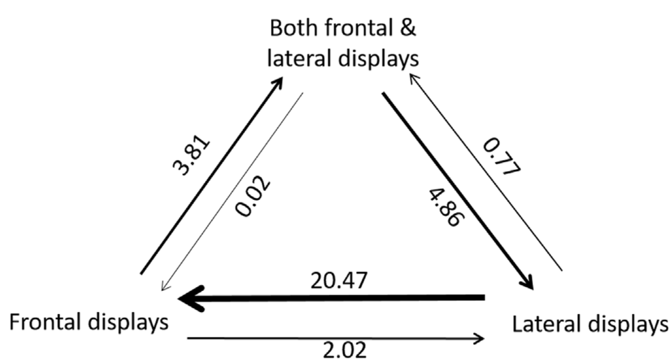

Fig. 3. Estimated transitions between three states: 'both frontal and lateral displays', 'frontal displays', and 'lateral displays'. Estimates are averages based on stochastic character mapping carried out on a sample of 100 phylogenetic trees (Revell, 2012). Directions of the arrows indicate transitions between states. Numbers and arrow thickness indicate the average number of transitions between states across all phylogenies.

Fisherian runaway (i.e. a positive loop between the female mate choice for the male trait and the resulted male extraordinary trait), but the diversity is maintained, and runaway does not occur (Beehler and Foster, 1988; Thery, 1992; Jiguet and Bretagnolle, 2006; Duraes et al., 2008). Many attempts have been made to explain it away, but the paradox remains. Therefore, studying courtship displays of these 'lekking' species under sexual selection theory to solve the 'lekking paradox' provides an avenue for further research.

As phylogenies are hypotheses about evolutionary relationships (Reynolds et al., 2002), the results and patterns of comparative studies based on phylogenetic relationships should be interpreted with caution. Despite the fact that we used courtship displays of 131 gallinaceous species in this study to investigate the origin and subsequent transitions of this trait in Galliformes, some limitations need to be considered. At best, data of 131 species from five families used in this study are representative of all species of Galliformes, and our results are complementary to various kinds of data from different sources that differ in quality. At worst, the inferences (the origin and subsequent transitions of courtship displays in Galliformes) might be biased. We still missed the courtship displays of more than 160 species; moreover, the courtship displays of some species we have used in this study might only be partially recorded. However, although some patterns would change as more information becomes available, we believe that the overall direction of our results is probably correct. It is worth noting that this kind of uncertainty is not unique to comparative studies using phylogenetic information; there are errors around all statistical estimates, including those derived from experimental studies.

5. Conclusions

Studies on Galliformes have demonstrated remarkable achievements since 1990, but life history information on many galliform species is still lacking, which has hindered conservation efforts and effectiveness. We showed that courtship displays in this avian group evolved from an origin of rather short and straightforward displays, including both frontal and lateral elements. This original state then evolved towards two extremes, either 'frontal displays' or 'lateral displays', with more complicated and elaborate display components. Moreover, subsequent transitions occurred from the state of 'lateral displays' to 'frontal displays' much more often than the other way around during the evolutionary history, indicating a positive selection of 'frontal displays'.

Contributions

DW designed the study; DW, XG and XR collected the data; DW analyzed the data; DW, XG, XR and GS wrote the manuscript. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.avrs.2022.100008.

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