

THE EVOLUTION OF TARSAL SPURS IN GALLIFORMES

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Abstract

Animal weaponry has long been of interest to biologists. While most birds lack structures that likely evolved specifically as weapons, birds in the order Galliformes (chickens, pheasants, and turkeys) are unique in possessing tarsal spurs. These horn-like structure located on the back of the tarsus vary vastly in size, shape and number between species – and although spurs are known worldwide for their role in male-male competition (see: cockfighting) spurs are also present in the females of many species. Using data collected from museum skins and published sources and a recent phylogeny of Galliformes, I found that tarsal spurs originated from a common ancestor in both males and females, and that there has been a rapid loss of tarsal spurs in females, whereas males have largely retained them. I also found evidence supporting the hypothesis that spurs in both males and females may have been favored by natural selection for reasons other than intraspecific fighting for mates (i.e. defense), and that male tarsal spur presence in Phasianidae is likely influenced by sexual selection.

Introduction

One of the few recorded instances of specialized weapons in birds are found within the Galliformes – a group of ground-feeding birds including Megapodiidae (brush turkeys), Cracidae (guans and curassows), Numididae (guinea fowl), Odontophoridae (New World quail), and Phasianidae (Old World quail, peafowl, and partridges, pheasants, turkeys, and other game birds). Many galliform species bear a horn-like structures found approximately 2/3 of the way down the posterior side of the tarsometatarsus known as the tarsal spur. These spurs may be any combination of sharp (Figure 1A) or dull (Figure 1B), and long (Figure 1A) or short (Figure 1B), and in some species, multiple spurs can be found on a single leg (Figure 1C). And, as recorded by archeologists

(Sadler, 1991; de Cupere et al., 2005; Serjeantson, 2009; Doherty, 2013) cockfighters (Dundes, 1994), and domestic farmers, (Darwin, 1871) tarsal spurs can cause significant damage to an opponent.

As with most animal weapons (Emlen, 2008), tarsal spurs are hypothesized to have been selected upon for use in the intrasexual fights of males competing for access to mating opportunities (e.g., Darwin 1871, Davison 1985, and Sullivan and Hillgarth 1991). However, the inconsistent pattern of spur presence and absence within within the two Galliformes families that tarsal spurs are found in (Numididae and Phasianidae) challenges the theory that intrasexual competition is their sole function. Spurs are found in the females of numerous species and the males of many monogamous species (both groups lacking the need for excessive or frequent intraspecific or intrasexual combative behavior), and are absent in many of the polygamous species that display highly aggressive competitive behavior, such as those found in Tetraoninae (grouse) (Davison, 1985; Crowe et al., 2006).

Despite these confounding observations, the literature focuses on the hypothesis that the basic function of tarsal spurs is intraspecific fighting, though there are some alternative hypotheses to explain the variability of presence in males as well as their presence in females. In the *Descent of Man* (1871), Darwin suggested spurs originated in males in response for the need for male-male competition, and suggested that female spurs were nothing more than a byproduct of their presence in males, stating the following:

“[T]he presence and absence of spurs in the females result from different laws of inheritance having prevailed, independently of natural selection. With the many females in which spurs appear as rudiments, we may conclude that some few of the successive

variations, through which they were developed in the males, occurred very early in life, and were as a consequence transferred to the females, in the other and much rarer cases, in which the females possess fully developed spurs, we may conclude that all the successive variations were transferred to them; and that they gradually acquired the inherited habit of not disturbing their nests.”

Alternatively, Davison (1985) provides a different hypothesis to the origin of female spurs. In a study examining over 2500 museum skins to assess spur presence, Davison concluded that spurs originated together at one time in both males and females, and that their condition was blunt, (i.e. not that natural selection may have originally favored spurs that stunned their opponent instead of fatally wounding them.) He mentioned in this and a subsequent 1986 paper that spurs could have a function in both males and females due to predator or territory defense, and noted the differences in spur characteristics of species living in different habitat. But ultimately, Davison also concluded that their original function was for intraspecific fighting, offering the hypothesis that over evolutionary time spurs were either lost if the need for fighting in both males and females disappeared, or selected upon to become longer and sharper as intense male-male competition increased.

Davison (1985, 1986) also emphasized the potential role between mating system and spur presence in both males and females – with higher rate of male spur presence being found in polygynous systems, and a higher rate of female spur presence being found in monogamous systems. Subsequently, there has been much discussion on the potential role of sexual selection on male spur presence and physical variability in phasianid species (von Schantz et al., 1989, Kirkpatrick 1989; Hillgarth, 1990; Göransson et al., 1990; Ligon et al., 1990; Wittzell, 1991; Mateos and Carranza, 1996; Buchholz, 1997; Badyaev et al., 1998; Hill, 2003; Papeschi and

Dessi-Fulgheri, 2013). But experimental evidence does not consistently support the hypothesis that spurs are used as an ornament displayed female preference, and a publication using phylogenetic controls (Sullivan and Hillgarth, 1993) was unable to conclude that either spur length or spur number is significantly related to mating system within phasianid species.

Lastly, contrary to Davison's 1985 conclusion that spurs evolved once in all Galliformes, Crowe et al.'s 2006 study examining spur presence/absence in a phylogenetic context and concluded that spurs have been gained at least twice for males within Galliformes, once in Numididae and once in Phasianidae. But since the time of that publication, our understanding of the relationships within Galliformes has changed (reviewed in Wang et al., 2013), and Crowe et al. did not conduct a separate test for the evolution of female spurs.

Thus, several questions about the origin and evolution of tarsal spurs remain unanswered:

1. In the context of recent phylogenetic data, is it more likely that tarsal spurs originated one or multiple times within Galliformes?;
2. Is spur presence in males or females dependent upon mating system or other potential correlates of sexual selection such as size dimorphism?;
3. Is spur presence in males or females dependent upon factors that would indicate a more defensive use (e.g. natural selection)?;
- and, 4. Do patterns of spur evolution differ within just Phasianidae as compared to Galliformes overall?

This study aims to answer these questions using a recent phylogeny of Galliformes and a thorough review of available data. In addition to providing a comprehensive overview of the rates of spur gains and losses in both Galliformes and Phasianidae, I have tested the dependence of spur presence upon a variety of non-spur variables, such as mating system (based on the discussions by Davison (1985) and Sullivan and Hillgarth (1993)), parental care system, habitat, and nesting location (to represent a potential selective pressure related to a need for defense), and

body size dimorphism (to represent a selective pressure related to sexual selection). An overview of the predictions for dependent relationships between these variables and spur presence in under the forces of either natural or sexual selection is provided in Table 1.

Methods

Spur presence or absence in either sex was coded for each species in the tree based on data from Davison (1985), Madge and McGowan (2002), and supplementary visits to museum collections (Florida Museum of Natural History, Louisiana State University Museum of Natural Science, and the Smithsonian National Museum of Natural History). Spur data was not obtained for 60 species, and there were 20 cases in which Davison and Madge and McGowan disagreed on the presence of female spurs, (15 where Madge and McGowan suggested females had spurs, and five where Davison suggested females had spurs). In species that have spurs in both sexes, spurs typically show up far less frequently in females (i.e. presence may be found in less than 10% of females in the population) than in males, and are usually much smaller in females than in males (Davison, 1985). Consequentially, their presence may not be identified if a relatively small number of specimens may be examined. As such, I coded *any* recorded instance of a spur presence as a “yes” for the species. Illustrating the challenges with identifying which species had spurs, I identified a female *Pternistis leucoscepus* with spurs, a species which neither Davison nor McGowan recorded as having female spurs.

In addition to spur presence and absence, to test for alternate explanations for tarsal spur origin, I coded the following variables into binary categories based upon data from previous publications (Davison, 1985; Dunning Jr., 1992; Cockburn, 2006; del Hoyo et al., 2018):

1. Mating System: monogamous (species suspected to be monogamous or largely monogamous) or non-monogamous
2. Parental Care System: evidence of bi-parental care, or no evidence of bi-parental care
3. Habitat: mostly open (grassland, desert, rocky areas, savanna, wetlands) or mostly closed (shrubland and forest)
4. Nesting Location: in/on/close to ground (not higher than 1m) or above ground (higher than 1m)
5. Body Size Dimorphism: coded as “yes” when $[\text{weight}(\text{male}) - \text{weight}(\text{female})] / \text{weight}(\text{female}) > .10$, and “no” when the difference in weights was $< .10$

Analyses

1. Test for Ancestral Reconstruction:

I used Mesquite (Version 3.4, Maddison and Maddison 2017) to reconstruct the ancestral condition for spur presence and absence in both males and females based on a phylogeny of Galliformes consisting of 264 species (Kimball et al., in prep) constructed using a super-matrix of mitochondrial and nuclear DNA. Using a likelihood ratio test incorporating branch lengths, I found the best model to explain the rates of gain and loss (Asymmetric 2-parameter model or MK1 model) within all Galliformes and Phasianidae only.

To determine if spurs originated once or multiple times, I used the model which best explained spur evolution within all Galliformes and recorded likelihood for the presence or absence of spurs at key nodes.

2. *Correlates of Spur Presence:*

To determine whether spurs were dependent upon the variables in Table 1, I used a test for correlated evolution of discrete characters (Pagel, 1994) as implemented in Mesquite, which measures the likelihood of dependence between two variables within a phylogenetic context.

In all cases, spurs were considered the dependent variable. Any species in which trait information could not be found were removed from that individual analysis. I measured the p-values from the output of 1000 simulations, and used a criterion of $p < 0.05$ to denote significance. Separate analyses were conducted for male spur presence and female spur presence. Because there has been discussion about the potential role of sexual selection just within Phasianidae, analyses were done both in the context of all Galliformes and of Phasianidae.

Results

Out of the 264 galliform species in the phylogeny, 113 had spurs and 151 lacked spurs. Of those 113 spurred species, 44 had spurs in both sexes. No species had spurs present in females alone. Spurs were only present in Numididae and Phasianidae, and were absent in Megapodiidae, Cracidae, and Odontophoridae (Figure 2).

The results of ancestral reconstruction test (Table 2) indicates that for all Galliformes, the Asymmetric 2-Parameter model best represents the data for both male ($p < 0.05$) and female ($p < 0.01$) spur presence. In both sexes, the rate of loss was higher than the rate of gain, with a gain:loss ratio of approximately 1:6.0 for males and 1:8.5 for females. For Phasianidae, the Asymmetric 2-Parameter model again best represented the data ($p < 0.01$), for females with a gain:loss ratio of approximately 1:3.3. However, the data for males was best described by the MK1 model, which indicated no significant difference between the rates of gains and losses of

spurs within that family. This result suggests that spurs in Phasianidae were largely maintained in males and successively lost in females over time. When I examined the likelihoods of spur presence or absence at each key ancestral node (reported in Table 3), results indicated that a single gain of spurs in both males and females was more likely, followed by a loss in the ancestor of Odontophoridae.

The results of the test for correlates of spur presence are listed in Table 4. Across all Galliformes, female spur presence was correlated with habitat, nesting location, and body size dimorphism, though there were no correlates of male spur presence. However, for Phasianidae only, male spur presence was correlated with body size dimorphism, but not mating system. These results support the hypotheses that females may have originally evolved (or at least maintained) spurs for a functional purpose such as nest or territory defense, and that sexual selection (at least as evidenced by size dimorphism) has likely played an important role in males within Phasianidae, but possibly not in the origin of spurs.

Discussion

I examined the presence and absence of tarsal spurs in a phylogenetic framework to answer questions about their origin and provide insights as to their functional history. The results support the conclusion of Davison (1985) that spurs likely evolved only once in Galliformes in the ancestor of Numididae, Odontophoridae, and Phasianidae. These results contradict Crowe et al (2006), who suggest spurs evolved independently in Numididae and Phasianidae.

I did not find any evidence supporting the hypothesis that spur presence in males or females is dependent upon mating system. This result supports a previous phylogenetic regression study by Sullivan and Hillgarth (1991), which found no significant relationship

between mating system and spur number and length. However, the mating system in many of these species is not well understood (Sullivan and Hillgarth, 1991), and it may be that incorrect classification of mating system may have obscured my ability (and that of Sullivan and Hillgarth 1991) to identify a link between these traits.

In males, spur presence was correlated body size dimorphism in phasianids – indicating that forces of sexual selection may be important. Sexual selection is known to be strong in many phasianid species (Darwin, 1871), but may not be as important outside of that family where many taxa are monomorphic. Thus, it is possible that the strong influence of sexual selection on male spur presence in Phasianidae, combined with a lack of a role for sexual selection and spur presence outside of Phasianidae, may explain why there was no clear correlates of spur presence in males for all Galliformes. For females, it is likely that spurs may have evolved for a functional use related to defense, but it is still plausible that they could have also been used in intraspecific competition for other resources, or for males during assortative mating within flocks, as suggested by Davison (1985).

As no significant correlations with female spur presence were found within Phasianidae, I am unable to provide an explanation as to why females may have retained spurs in only select species within that family. It is possible that for some species, spurs are vestigial structures. In my observations of specimens, spurs in females were typically blunt, even when males of the same species had sharp spurs. Future analyses may want to survey and quantitatively score variables indicating the relative utility of spurs in a species (e.g. number, length in relation to body size, and “sharpness”), and also measure the relative abundance of tarsal spur presence within that species for both adult males and females to help answer questions about their retention in some species.

Lastly, there is reason to believe that spur development is different in females due to the failure of the bony core to completely ossify to the hypotarsal ridge (Figure 3) or the lack of a bony core entirely. Though information and discussion on spur development has drastically increased in the last century thanks to researchers such as Goodale (1918, 1925), Kozelka (1929, 1933a, 1933b), Domm (1931), Juhn (1946, 1952); Quigley and Juhn (1951), Holman, (1964), Washburn and Smyth (1971), Lucas and Stettenheim (1972), Christmas and Harms (1981), West (1985), Sadler (1991), Briganti et al. (2002), Ohlsson et al. (2002), and Serajeston (2009), with the majority of research has been conducted on males within Phasianidae (and restricted to a very limited number of species.) Increasing our understanding of the development of tarsal spurs in females would also be valuable in discussing the potential function and utility of female spurs particularly.

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Table 1: Predicted Relationships Between Variables

Non-Spur Variable	Natural Selection on Male Spur Presence	Natural Selection on Female Spur Presence	Sexual Selection on Male Spur Presence
Mating System	No	No	Yes, especially within Phasianidae
Parental Care System	Yes, potential use in in biparental care systems for nest defense	No	No
Habitat	Yes, potential use as a defensive weapon in more open habitats	Yes, potential use as a defensive weapon in more open habitats	No
Nesting Location	Yes, potential use in biparental care systems for nest defense of ground nesters	Yes, potential use for nest defense of ground nesters	No
Body Size Dimorphism	No	No	Yes, especially within Phasianidae

Table 2: Ancestral Reconstruction Outputs

Output	Male Spur Presence in all of Galliformes	Female Spur Presence in all of Galliformes	Male Spur Presence in Phasianidae Only	Female Spur Presence in Phasianidae Only
MK1 Model -Log Likelihood	45.414	102.894	32.284	84.741
Asymmetric 2- Parameter Model -Log Likelihood	43.313	92.587	31.925	80.522
Difference	2.100	10.307	0.359	4.219
Chi-square Statistic	4.200	20.615	0.718	8.437
P-value	< 0.05	< 0.01	< 0.9	< 0.01
Favored Model	Asymmetric 2-Parameter	Asymmetric 2-Parameter	MK1	Asymmetric 2-Parameter
Asymmetric Model Forward Rate	0.324	1.414	N/A	4.229
Asymmetric Model Backward Rate	1.974	12.040	N/A	13.186

Table 3: Likelihood Values for Spur Absence/Presence at Important Nodes

Ancestral Node of	Likelihood of Spur Absence in Males	Likelihood of Spur Presence in Males	Likelihood of Spur Absence in Females	Likelihood of Spur Presence in Females
All Galliformes	0.91	0.09	0.83	0.17
Numididae, Odontophoridae, and Phasianidae	0.30	0.70	0.16	0.84
Numididae	0.07	0.93	0.04	0.96
Odontophoridae and Phasianidae	0.31	0.69	0.15	0.85
Odontophoridae	0.77	0.23	0.45	0.55
Phasianidae	0.24	0.76	0.09	0.91

Table 4: P-values for Pagel's 1994 Correlation Tests*

Non-Spur Variable	Male Spur Presence in all of Galliformes	Female Spur Presence in all of Galliformes	Male Spur Presence in Phasianidae Only	Female Spur Presence in Phasianidae Only
Mating System	0.353	0.067	0.557	0.484
Parental Care System	0.223	0.223	0.733	0.067
Habitat	0.187	0.008	0.312	0.134
Nesting Location	0.189	0.017	0.054	0.115
Body Size Dimorphism	0.138	0.030	0.001	0.226

*significant results are bolded

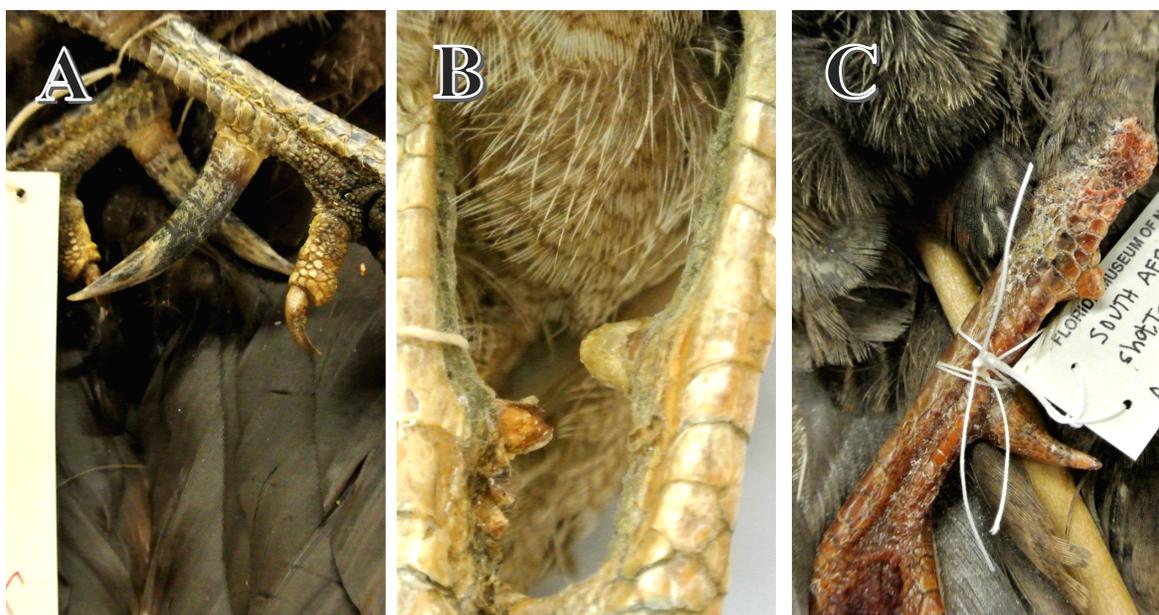


Figure 1: Examples of variability in spur morphology. A. *Gallus gallus*; B. *Francolinus adspersus*; C. *Francolinus* after. All specimens photographed were male. Photographs were taken at the Florida Museum of Natural History.

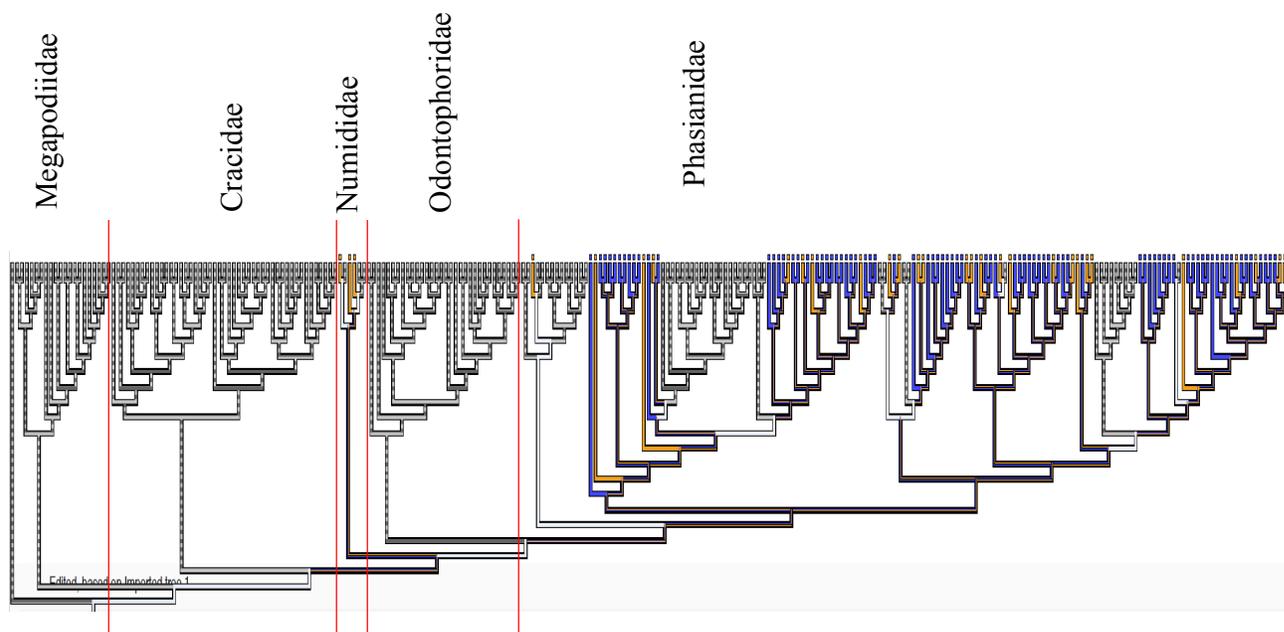


Figure 2: Tree showing tarsal spur presence in males and females of galliform species. Blue represents spur presence in males of the species only. Orange represents spur presence in both males and females. Black/grey stripes indicate spur absence in both males and females.



Figure 3: Photograph showing the absence of an ossified bony core in female tarsal spurs of *Pavo muticus*. Photograph taken at the United States Museum of Natural History.