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Investigating Behavioral Patterns in Birds with Wing Weaponry and Skeletal Weaponization in Two Zenaida Doves

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INVESTIGATING BEHAVIORAL PATTERNS IN BIRDS WITH WING WEAPONRY AND SKELETAL WEAPONIZATION IN TWO *ZENAIDA* DOVES

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Chapter One:
Behavioral Patterns in Birds
with Wing Weapons

Introduction

When one thinks of aggression in birds, images of sharp beaks and talons may come to mind. However, domestic pigeon keepers, and anyone who has ever been attacked by a goose, can attest that there is another form of aggression some birds use quite effectively: the wing-slap. Although the exact implementation of this behavior can vary from species to species, it typically involves the lifting of the wings, followed by an aggressive strike at an opponent with the closest wing or buffeting with both. Wing-slapping is commonly observed in waterfowl as well as pigeons and doves, but exists in many other species. (Lucas, 1893; Rand, 1954; Johnston, 1960,1964; Harrison, 1961; Goodwin, 1983; Livezey & Humphrey, 1984; Barrow et al., 1986; Swanson & Rappole, 1993; Buchholz, 1997; Murton & Isaacson, 2008; Fronimos, 2011; Almaguer, 2012; Hume & Steel, 2013; Menezes & Palaoro, 2022).

This form of aggression is often associated with weaponizing modifications to bones of the wings. Despite numerous studies of Aves in ecological research, investigations into the occurrence of weapons is infrequently extended to birds. This may simply be a result of the relative rarity of weapons in birds, as less than 2% of bird species show the kind of combat specified boney weapons I focus on here. Of this small percentage, less than half are wing weapons - the rest are tarsal spurs (Menezes & Palaoro, 2021). There are 53 avian species with rigorously documented weaponizing wing modifications, and at least 70 others in which modification is suspected (Menezes & Palaoro, 2021). These wing modifications may take the form of sharp, pointed spurs, or of blunt, clublike knobs (Fig 1.). The majority of such modifications are to the extensor process of the carpometacarpus bone (Fig. 2). (Rand, 1954; Menezes & Palaoro, 2022). This bone is a fusion of carpal and metacarpal bones that supports the portion of a bird's wing distal to the carpal (wrist) joint. The extensor process serves as an attachment point for extensor muscles in the wing and ligaments supporting the patagial region of the extended wing. In many birds with modifications for wing-slapping, this process has been co-opted as a weapon. Inflation or extension of the extensor process of the carpometacarpus creates the core of most wing weaponry across avian taxa.

Although some of the more extravagant forms of wing weaponization have long been of interest to researchers, the behavioral context and fitness consequences of bearing and utilizing these traits have only recently begun to be explored. At the time of writing, no studies have explicitly explored the behavioral context of the wing-slap, and only one study has empirically investigated behavioral contexts surrounding boney weaponry across avian taxa (Menezes & Palaoro, 2022). Menezes and Palaoro (2022) present evidence that boney weaponization in birds, including both carpal and tarsal weaponization, is less common in species that are adapted to be highly volant. They imply that weaponry is selected against in birds relying on sustained flight, such as long-distance migrators, as well birds relying on energetic daily flight, like hummingbirds. Menezes and Palaoro provide mathematical evidence that the additional weight of boney weapons can significantly increase the cost of powered flight, especially in small birds. A functional weapon in a small bird may make up a greater proportion of its body mass, thus disproportionately affecting flight. Additionally, larger birds are more efficient at translating metabolic power into mechanical power in flight (Ward et al., 2001; Videler, 2005; Guigueno et al., 2019). This increased efficiency may provide a buffer to the energetic costs of wing weapons in larger birds compared to smaller birds. While Menezes and Palaoro's recent work is highly influential in our understanding of weaponization in birds, its singularity highlights the lack of information about large-scale context for wing weapons across avian taxa.

In this review, I present information on what is known about the behavioral context of wing weaponry, and do so using a framework built on the ecological and behavioral factors that favor weaponization in other, non-avian, taxa (Emlen, 2008). Although the energetic cost associated with weapons described by Menezes & Palaoro (2022) may explain some of the variability in the occurrence of wing weaponry, understanding costs alone cannot provide a full picture of how these traits evolve. To understand the benefits of bearing a weapon, we must examine various aspects of avian ecology and social behavior. I focus this review on resource defense, as I expect that most avian weapons serve this purpose (Andersson, 1994).

I present behavioral patterns across 53 avian species, representative of 6 families that possess well documented wing weaponry, with a focus on space and resource defense over time. For each weaponized avian species, I have compiled available observations relating to mating systems, non-breeding sociality, space use, and dependency on flight and migration (Table 1). Parenthetical numbers reference row numbers for species information in Table 1. It is important to note that many other species likely possess wing weapons, sometimes subtle in form, and as such, this review provides conservative estimates of avian weaponization.

Patterns of Weaponry Across Taxa

The evolution of weaponry is intimately tied to space use, resource use, and social structure across taxa (Emlen, 2008; Rico Guevara & Hurme, 2018). Comprehensive reviews of non-avian weapons used in intraspecific combat find that weapons are almost entirely limited to species in which resource-defense or female-defense mating/space systems are used (Emlen, 2008), and reviews with limited representation of wing weapons reiterate this observation (Rico-Guevara & Hurme, 2018). The most developed of such weapons are found in species that are herbivorous or feed on small invertebrates, and thus lack predatory adaptations that might be used in combat (Rico-Guevara & Hurme, 2018). In other words, a species with large teeth or sharp claws used for hunting need not develop additional weaponry to defend resources, whereas species lacking these features require specific adaptations for physical combat.

Out of all weapon-bearing taxa, ungulate mammals are likely the best explored, and exemplify patterns observed across taxa (Emlen, 2008). In most ungulate species, only males possess weaponry, which is used to defend groups of females or patches of resources against rival males. By defending harems of potential mates, or the resources that potential mates need to survive, an individual male greatly increases his potential reproductive output compared to rivals. Similar to a male ungulate that defends a feeding space for a herd of females, males of many weapon-bearing invertebrate species, and even some amphibians, defend burrows used for nesting by females (Emlen, 2008). In these weapon-bearing species, polygyny is common and sexual dimorphism is often pronounced (Geist, 1977; Emlen, 2008).

If patterns of weaponization observed in non-avian taxa hold true in Aves, we would expect wing weaponry to be primarily present in male birds, and that these males would aggressively defend patches of limited resources to attract potential mates. We would also expect species with wing weapons to more likely be herbivores or insectivores, rather than birds of prey. Additionally, given the increased energetic cost of weaponry in small, highly volant birds, we would expect species which are most dependent on flight (e.g., migratory species) would only bear wing weapons if resource competition was extreme, or if they were large bodied, and thus able to better sustain the cost of weaponization (Menezes & Palaoro, 2022).

Mating and Space Use in Birds with Wing Weaponry

Of the 53 species reviewed here, only one falls into the common non-avian pattern of resource-defense polygyny. The knob-billed duck (*Sarkidiornis melanotos*)(18), a species that possesses pronounced carpal knobs, has transient seasonal pair bonds and is frequently polygynous (Brown, Urban, & Newman, 1982; Safford & Hawkins, 2013). Males establish seasonal breeding territories encompassing nesting sites to which they attract and subsequently defend a harem of females (Dallmeier & Cringan, 1989). Females within each breeding group aggressively establish dominance hierarchies (Brown, Urban, & Newman, 1982; Safford & Hawkins, 2013). This species strays from the norm of monogamy in waterfowl and appears to rely on aggressive interactions primarily to establish exclusive access to a group of mates. It is unclear if weaponry in this species is highly sexually dimorphic, but significantly more pronounced weapons in males would be consistent with the behavior observed in this species.

Reviews of non-avian weaponry have identified female-defense strategies as common context for development of weaponry, but when including birds, mate-defense is a more accurate term due to the full reversal of sex roles in *Jacanidae*. Three species within this family (47-49) possess carpal spurs, while another four (50-53) display carpal knobs, and unique, flattened, blade-like radii (Fig. 3). It has been proposed that this structure is adapted for non-combat purposes, including the odd Jacanid behavior of carrying chicks under the wings (Fry, 1983b). However, chick-carrying behavior is present in species that do not have modified radii, so it seems more likely that this modification is related to combat (Tarboton & Fry, 1986; Winkler, Billerman & Lovette, 2020).

All seven weaponized species of jacana are polyandrous (Jenni & Collier, 1972; Wrege, & Webster, 1998; Seddon & Ekstrom, 1999; Butchart, 2000; Mace, 2000; Emlen, 2008;

Butchart, Dowsett-Lamaire & Dowsett, 2014; Jenni & Kirwan, 2020a,c,d). Female jacanas vigorously defend multi-purpose breeding territories that encompass the smaller defended territories of multiple males (Jenni & Collier, 1972; van Balen & Prentice, 1997; Emlen, Wrege, & Webster, 1998; Butchart, Seddon & Ekstrom, 1999; Wells, 1999; Butchart, 2000; Mace, 2000; Pacheco & Piratelli, 2005; Dowsett-Lamaire & Dowsett, 2014; Jenni & Mace, 2020; Jenni & Kirwan, 2020a,c,d). Individuals are highly aggressive against members of their own sex, and non-territorial individuals are essentially excluded from breeding. When a territory-holding female is deposed, the new territory holder frequently inherits all of the previous female's mates. Interestingly, the lesser jacana (*Microparra capensis*), the one species that lacks weaponized radii or prominent spurs, is monogamous, and noted to be territorial, but less aggressive than other species (Tarboton & Fry, 1986; Hustler, 2002; Jenni & Kirwan, 2020b). This seems to imply that weaponization in this family is related to monopolizing access to mates rather than excluding conspecifics from use of territorial resources. Weaponry in jacanas is known to be sexually dimorphic, with females possessing larger carpal spurs than males (Emlen & Wrege, 2004).

The eight species reviewed thus far show patterns of behavior comparable to those observed in weapon-bearing non-avian species: a single individual of one sex maintains exclusive mating opportunities with members of the opposite sex through defense of groups of mates and the resources they require. However, the majority of birds with wing weapons are not so similar to non-avian taxa. As previous literature focused on tarsal weaponry has observed, there is a glaring difference in the social structure of most birds compared to weapon-bearing non-avian taxa: monogamous mating systems (Geist, 1977).

Among weapon-bearing members of *Anatidae* (1-26), a family with diverse wing weaponry including wing spurs and carpal knobs, monogamy is the norm. Of the 26 Anatid species reviewed here, 24 are known to hold territories that are defended by a continuously monogamous pair. Although there are some instances of defense extending only to nest-specific sites or winter feeding territories, as in the greater white-fronted goose (Anser albifrons)(4), ruddy shelduck (Tadorna ferruginea)(23), and common shelduck (Tadorna tadorna)(24), the majority of cases involve defense of multi-purpose breeding territories on which adults live and feed. Six species are known to remain on their defended territories year-round (3, 12, 13, 19, 20, 21), and at least 5 others (7, 8, 24, 25, 26) return to the same territory year after year. Almost all species that are not year-round territory holders form gregarious flocks in the non-breeding season.

Anhimidae, a sister group to *Anatidae*, consists of only three species, all of which have wing spurs (27-29). All three species in this family exhibit long-term monogamy and defend multi-purpose breeding territories year-round (Stonor, 1939; Barrow, Black & Walter, 1986; Naranjo, 1986; Carboneras, 1992b; Kear, 2005).

The family *Charadriiae* consists of ten genera of plovers and lapwings, but only one of these genera includes birds with well documented wing weaponization (30-42). All of these species are members of the genus *Vanellus* and all have wing spurs. Similar to weapon-bearing Anatids and Anhimids, *Vanellus* lapwings are monogamous and territorial during breeding season. At least some species participate in cooperative breeding, indicating that family bonds last beyond a single season (Cerboncini et al., 2020). *Charadriiae* genera without wing weapons typically have less structured pair bonds and less vigorous territorial defense against conspecifics (Billerman, Winkler & Lovette, 2020).

Chionidae is a small family that includes only two species, both of which are spurred coastal scavengers. Like the majority of species reviewed, the snowy sheathbill (*Chionis albus*)(43) and the black-faced sheathbill (*Chionis minor*)(44) exhibit long-term monogamy and defense of multi-purpose breeding territories. The black-faced sheathbill may defend the same territory year-round (Bried & Jouventin, 1997).

Long-term monogamy is by far the most common mating strategy in birds with wing weapons, which is not consistent with patterns of weapon occurrence outside of Aves. In most non-avian animals, and particularly ungulates, weapons adapted for intraspecific aggression are exclusive to, or much more pronounced in, males. These weapons are hypothesized to have evolved in association with increased male-male competition as species colonized environments where resource access, and therefore mate access, could be highly monopolized (Geist, 1977, Emlen, 2008; Rico-Guevara & Hurme, 2018). This explanation is relatively consistent with behavioral patterns observed in Jacanas, and in the knob-billed duck. However, in general, birds with wing weapons are monogamous species with long-term bonds in which both males and females possess weaponry and participate in territorial defense.

The prevalence of biparental care in birds may provide some explanation for this observation (Geist, 1977). Biparental care is far more common in Aves than in other taxa, with an estimated 81% of species displaying this behavior (Cockburn, 2006). In non-avian species, it is reasonable for a male to expend a great deal of energy defending patchy resources to attract females and maximize his reproductive potential, because his energetic commitment to his breeding partner and offspring does not extend beyond this defense. However, in non-avian species it is much less common (or even impossible, in the case of mammals) for males to provide a comparable level of parental care to that provided by the female (Clutton-Brock, 1991). In most birds, both parents bear the energetic cost of caring for offspring, therefor the male cannot devote as much time and energy to maintaining exclusive resource access. In relation to large predatory species, it has been noted that if the survival of each individual depends on resources tied to a defended territory, both males and females should be adapted for defense (Rico-Guevara & Hurme, 2018). I believe that this tenant can be applied to birds as well. In the many of species reviewed, resources on a multi-purpose breeding territory are needed not only for reproduction, but survival of the breeding pair. As both individuals contribute to parental care, it is logical that females would sometimes be required to contribute to territorial defense when males are otherwise occupied, and this is the pattern we see in many birds with wing weapons. Furthermore, many weapon-bearing species are non-migratory birds that defend territories year-round. It seems that, in many of the birds reviewed, the primary pressure for the development of wing weaponry is the necessity and ability to defend patchy, specialized resources year-round or seasonally for many contiguous years.

Steamer ducks (19-21) provide an excellent illustration of this interpretation. The Falkland steamer duck (*Tachyeres brachypterus*), flightless steamer duck (*Tachyeres pteneres)* and flying steamer duck (*Tachyeres patachonicus*) are highly aggressive, using prominent carpal knobs in defense of their breeding territories (Livezey & Humphrey, 1985; Nuechterlein & Storer, 1985). Steamer ducks are relatively large waterfowl that are sedentary or near-flightless, and native to coastal regions of Argentina, Chile, and the Falkland Islands (Winkler, Billerman, & Lovette, 2020). These birds are monogamous, forming long-term (possibly life-long) pair bonds (Kear, 2005). Steamer duck pairs are known to defend their territory year-round. Both males and females participate in defense of contiguous swaths of territory, often along coastline or shoreline of inland water bodies. Defense is rigorous against both intra- and interspecific invaders and has been observed to result in severe injuries, including broken bones, and death of opponents (Livezey & Humphrey, 1985, Nuechterlein & Storer, 1985). It has been postulated that the combination of the birds' size and well-developed carpal knobs give them such an advantage in combat that there is little appreciable cost to attacking and driving smaller species out of their territories. This creates highly exclusive use of resources, and displays fitness to conspecifics (Nuechterlein & Storer, 1985). The stationary and predictable nature of patches of habitat for the aquatic invertebrates on which these ducks feed, combined with relatively stable year-round climate, creates an environment which makes it possible for a large benefit to be reaped by defending year-round territories against avian competition, conspecific or otherwise (Livezey & Humphrey, 1985).

The ecological setting described above has fostered the development of carpal weaponry in steamer ducks, and similar factors have likely influenced weapon development in other species as well. Similar settings where year-round defense is possible exist in many Southern hemisphere and equatorial regions, which may contribute to the over-representation of birds with wing weapons in these regions compared to the Northern hemisphere. River specialist ducks also fit into the pattern of specialized resource defense by pairs as a driving factor in avian weapon development. The African black duck (*Anas sparsa*)(3), the blue duck (*Hymenolaimus malacorhynchos*)(12) and the torrent duck (*Merganetta armata*)(13) are all river specialists possessing carpal weapons. The linear canyon or riverbank territories these species defend are highly specialized, required for breeding, and defended over long periods of time, once again creating an environment conducive to weapon development (Ball et al., 1978; Triggs et al., 1992; Williams & McKinney, 1996; Kear, 2005; Ippi et al., 2018). Even opportunistic sheathbill species are influenced by the necessity of specialized resource defense. Sheathbills live in far-south environments where food is sparse, so they depend greatly on the refuse of pinnipeds and seabirds for nutrition. These birds use their spurs to defend coveted territories within in seabird or pinniped colonies where consistent food is available (Parmalee, 1992; Forster, 1996; Jouventin, Bried, & Ausilio, 1996). Based on the species reviewed here, defense of specialized resources over long periods of time by bonded pairs of birds creates an environment conducive to the development of wing weaponry.

Flight in Birds with Wing Weaponry

Based on the work of Menezes & Palaoro (2022), we would expect most weaponized birds to be sedentary (remaining in the same general area for life after dispersal from natal space) or possibly nomadic (movement, usually short distance, in response to changes in resource availability, ie. water). However, we find that a significant fraction of species reviewed are migratory. Anhimids (28-30) are known to be sedentary and relatively terrestrial (Carboneras, 1992a; Naranjo, 1986; Carboneras et al., 2020), and weapon-bearing Columbids (45, 46) are thought to be sedentary (Goodwin, 1983; Serra et al., 2018; Baptista &… Bonan et al., 2020), but all other families reviewed have at least one migratory species.

Approximately 1/3 of the Anatid (1-26) species reviewed exhibited some kind of migratory behavior (although more frequently regional than long-distance). This is somewhat surprising considering the suspected selection against weaponry in highly volant birds (Menezes & Palaoro, 2021). Interestingly, there do not appear to be substantial differences in the behavior or ecology of more and less volant weapon-bearing Anatids. One possible explanation for the existence of wing weaponry in long-distance migrants, and also for the commonness of wing weaponry in Anatids in general is the large body size of these birds. Although ecological dependency on strong flight would appear to result in selection against weaponry, this effect is tempered by body size. Larger birds are more efficient during flight than smaller birds, which may become especially relevant in long-distance migration (Ward et al., 2001; Videler, 2005; Guigueno et al., 2019). Also, as previously noted, it has also been found that large body size is associated with higher likelihood of more or larger weapons in birds (Menezes & Palaoro, 2022). It is quite possible that large species, like most waterfowl, experience weaker selective pressure against spurs due to energetic cost in flight because they already have greater flight efficiency than smaller species.

All *Vanellus* species reviewed are sedentary to nomadic, with the exception of the Gray-headed lapwing (*Vanellus cinereus*) (41). However, body size may once again come into play. The migratory Gray-headed lapwing has the highest body mass of the *Vanellus* species considered here (Winkler, Billerman & Lovette, 2020). The Southern lapwing (*Vanellus chilensis*)(30) is the nearest in size to the gray-headed lapwing, but this sedentary and relatively terrestrial species has much more prominent spurs than its migratory relative. This further supports the idea that while the weight of spurs is a major tradeoff in highly volant birds, large body size can temper the effects.

Other Ecological Patterns in Birds with Wing Weaponry

A number of other general patterns appear in wing-weapon-bearing birds. First, as predicted, there are no highly predatory species represented here. Weapon-bearing species are either herbivorous, eat small invertebrates or eat carrion and other refuse. This is consistent with expectations that predatory animals possess morphological characteristics that serve a double purpose in hunting as well as in intraspecific aggression, therefore do not develop additional weapons used primarily in intraspecific combat.

Several interesting patterns, unrelated to initial predictions, were identified among the species reviewed. The majority of known weapon-bearing species reside in the Southern hemisphere. In fact, less than 10% of the reviewed species reside primarily in the Northern hemisphere. It is possible that this hemispheric difference is due to the differences in migratory patterns between Northern and Southern hemisphere birds. Birds in the Southern hemisphere are less likely to migrate than those in the Northern hemisphere, and those birds that do migrate typically migrate shorter distances (Dingle, 2008). Due to a more mild climate in much of the Southern hemisphere, long-distance migration is less advantageous for southern species. These species are more greatly affected by rainfall than seasonal temperature changes, which we see in the high proportion of nomadic species reviewed. Migratory habits should create selective pressure against wing weaponry in birds, which may explain the relative lack of weaponization in northern species.

In addition to occurring mainly in the Southern hemisphere, weapon-bearing birds are typically found near water. With the exception of two Columbid species, birds with documented wing weapons are waterbirds or shorebirds. I postulate that this is due to the specialized nature of high-quality territory for these species. Although every species clearly must have habitat preferences, such habitat is typically spread out over large, two-dimensional spaces. This is unlikely to be the case in species that form territories on the shores of bodies of water, where linear territory connectivity is more likely. Although several Anatid and lapwing species seem content with grassland habitat regardless of water access, the majority of species reviewed here ideally establish habitats either on the shores of large water bodies or wetlands, along coastlines, or in an area that encompasses the entirety of a small water body. Territories encompassing part of a body of water or shoreline are inevitably going to come in contact with other conspecific territories if population density is sufficiently high, and competition for this somewhat niche habitat is likely to be intense in many spaces. Additionally, lack of territory entirely excludes the possibility of breeding in many these species. This combination of factors may contribute to the development of wing weapons in waterbirds and shorebirds.

Behavioral Outliers

As with any association of behaviors, there is a spectrum of intensity within the patterns reported here. While many species with wing weapons defend multi-purpose territories year-round or consistently over many years (particularly those with highly-developed weapons), some species may defend smaller spaces, focused on the nest (4, 5, 24, 38). Many species are specifically noted to be highly aggressive, but in some cases, physical altercations are rare (4, 5, 30, 34, 35). The majority of species are sedentary to nomadic, and migrators are typically regional, but a few anatid species migrate long distances (4, 5). Although relatively consistent behavioral patterns can be determined for birds with wing weapons, there are always outliers, and our understanding of weaponry in birds would benefit from contextual studies of these species. A few of these outliers are highlighted below with brief suggestions for further research into why they differ from other weapon-bearing birds.

The spur-winged goose (*Plectropterus gambensis*)(16) possesses one of the largest spurs of all Anatids (Rand, 1954), and is singular among weaponized birds in that its spur is not a modification of the carpometacarpus bone, but rather of the radial bone in the carpal joint (Menezes & Palaoro, 2021). This species is also an outlier in its behavior. The spur winged goose has not been observed to exhibit any significant pair bonding, seasonal or otherwise (Brown, Urban, & Newman, 1982; Johnsgard, 2010). There is evidence that males may display some degree of mate-guarding behavior and occasionally temporary nest guarding behavior, but certainly not the long-term territoriality generally observed in weapon-bearing birds (Rand, 1954; Johnsgard, 1965, Brown, Urban & Newman, 1982). Given the large size and prominence of this species' spurs, the relative lack of apparent aggression in mating and nesting behavior is somewhat confusing. As a sedentary species, spur-winged geese likely do not experience as much selective pressure against the development of large spurs as many other Anatids might, but that alone clearly cannot explain their highly prominent wing spurs. I predict that direct male-male competition may occur in this species and has simply not been widely documented. More extensive research into the aggressive behavior of this species would prove enlightening.

There are also a few outliers in the patterns observed in flight behavior and size of weaponized birds. The snowy sheathbill breeds on the Antarctic peninsula but is found in southern South America outside of breeding season, whereas the black-faced sheathbill is sedentary and may defend year-round territory (Bried & Jouventin, 1997; Fang, 2020). The difference in movement patterns is less easily explained than in other groups, as the two species are similar in size and spur prominence. Although species in this family are still relatively large compared to many other birds they do not reach the size of migratory Anatids reviewed here (Billerman, Winkler & Lovette, 2020). Given the support for the cost of wing weaponry in highly volant birds, and for the additional cost to smaller bodied birds, further research into spur comparison between the migratory and sedentary sheathbill species could be quite interesting.

In a similar vein to the migration differences in sheathbills, jacanas are sedentary to nomadic, with the exception of the regionally migratory pheasant-tailed jacana (Howell & Webb, 1995; Gatter, 1997; Dostine & Morton, 2000; Spierenburg, 2005; Ash & Atkins, 2009; McCrary et al., 2009; Safford & Hawkins, 2013; Dowsett-Lamaire & Dowsett, 2014; Jenni & Kirwan, 2020a,c,d; Jenni & Mace, 2020). The pheasant-tailed jacana does not have larger body mass than other members of *Jacanadae*, but it is possible that the degree of aggression necessary for successful breeding in this family has created an environment in which the combat benefit of spurs is worth the energetic cost that may be incurred during regional migration. Further research into the effects of selective pressures on weapons in polygynous bird species like jacanas compared to more typical weapon-bearing birds is necessary to investigate this topic.

Unweaponized Birds

Given the comparative dearth of information on obvious weapons in birds compared to other taxa, it is unsurprising that little research has been done to define species which lack weaponry. Because weapons in many knob-bearing species are cryptic, it is difficult to say with confidence that a species lacks spurs without explicit morphological research, particularly within families where other weapon-bearing species are known to exist. There are, however, a few Anatids for which there is high confidence data that wing weaponry does not exist (Menezes & Palaoro, 2021). The freckled duck (*Stictonetta naevosa*)(55) and the white-backed duck (*Thalassornis leuconotus*)(56) are relatively gregarious birds that display little to no territoriality, consistent with their lack of weapons (Marchant & Higgins, 1990; Kear, 2005; Carbonera & Kirwan, 2020). This provides an interesting comparison with the reviewed weapon-bearing Anatids which were generally very aggressive. The last unweaponized species I will discuss, the Coscoroba swan (*Coscoroba coscoroba*)(54), another Anatid, is known to be highly aggressive and monogamous, like most weapon-bearing Anatids (Kear, 2005; Silva Garcia & Brewer, 2007). It is a regionally migratory species, but so are several weapon-bearing anatids of similar size (Kear, 2005). This species seems to be somewhat of an enigma within the predicted patterns of weaponization in Aves. The behavioral patterns of the Coscoroba swan likely exist within other Anatids that do not possess weapons, therefore it is important that future morphological and ecological research explores additional factors that differentiate weapon-bearing from weaponless Anatids.

Summary

The majority of weapon-bearing species reviewed here differ from weaponized non-avian taxa primarily in their mating system. It seems that the driver of wing weapon development is the ability and necessity to defend patchy, specialized resources or habitat as a breeding pair, particularly if the same space is defended year-round or over several consecutive years. The prevalence of biparental care in Aves may be a factor contributing to the importance of pair defense of specialized resources, and also in the presence of comparable weaponry in both males and females. These behavioral patterns are exemplified by steamer ducks and sheathbills, in which pairs which aggressively defend patches of feeding resources over long periods, and by river specialist ducks which establish year-round territories in coveted riverbank habitat. The prevalence of mild climates and resources that are defensible year-round in Southern hemisphere and equatorial habitats may contribute to the disproportionate number of weapon-bearing species in these regions compared to the Northern hemisphere.

There are a few weaponized avian species that exhibit behavior patterns similar to the multi-mate defense strategies common in non-avian species. This is seen primarily in the sex-role-reversed *Jacanidae*, in which females defend a large territory that encompasses the smaller territories of a harem of males. The polygynous behavior of the knob-billed duck also matches this pattern. However, in weaponized Aves, it seems that resource-defense polygyny is the exception, not the rule.

The majority of species reviewed are sedentary to nomadic birds that do not rely on being highly volant for components of their life history. This is also consistent with the lack of weapon-bearing birds in the Northern hemisphere, as migration plays a greater role in the behavioral strategies of Northern hemisphere birds compared to Southern hemisphere birds. There are, however, several migratory weapon-bearing species, particularly within *Anatidae*. This pattern may be explained by large body size in these species, which is associated with flight efficiency that may offset the energetic cost incurred due to the weight of wing weapons. Indeed, the majority of families reviewed here are medium sized or large birds, and there is little evidence of wing weaponry or wing related aggression in the multitude of small avian species. Interestingly, the taxa reviewed here are not known for the complex song that is present in many Aves (Billerman et al., 2020). It is possible that smaller birds are more limited in their ability to bear the cost of heavy weaponry and have instead adapted to funnel their resources into non-physical aggressive display. This is consistent with some data indicating that all Aves descend from a spur-bearing ancestor (Menezes & Palaoro, 2022).

In summary birds with wing weapons are typically large, sedentary, non-predatory species that participate in highly aggressive resource or mate defense. Newly explored here are possible explanations for the patterns that birds with wing weapons are mostly waterbirds or shorebirds and are almost exclusively found in the Southern hemisphere. With the exception of sparse Columbid species, pronounced wing weaponry occurs exclusively in the orders *Anseriformes* and *Charadriiformes*. A few weapon-bearing species offer exceptions to the patterns of monogamy and territoriality generally observed in birds with wing weapons, such as the spur-winged goose, but typically, common patterns are followed. Finally, the vast majority of avian species lack any kind of research into osteological weapons like wing spurs and carpal knobs. Further research into the definitive presence or absence of such weapons in additional avian species will be integral to our understanding of the ecological aspects and evolutionary history of weapons in birds.

Figures & Appendix

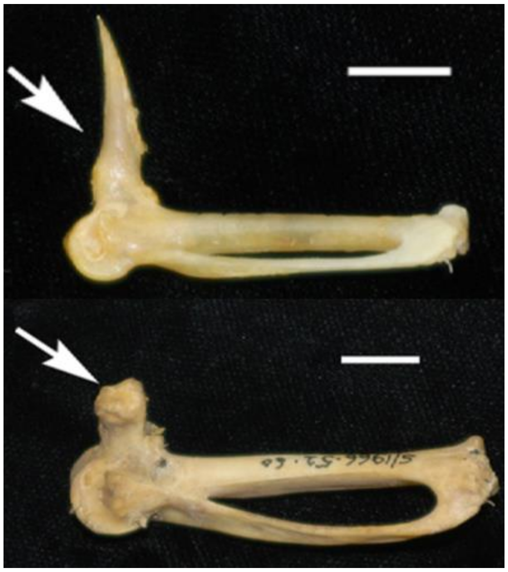

Figure 1:
On the top, the carpal spur of the masked lapwing (*Vanellus novaehollandiae*).
On the bottom, the carpal knob of the flightless steamer duck (*Tachyeres pteneres*).
Modified from Hume & Steel, 2013.

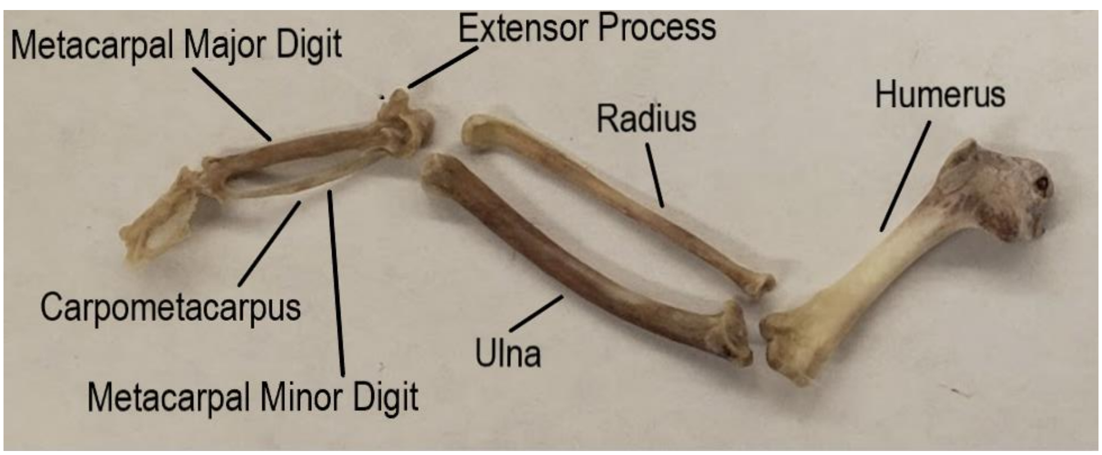

Figure 2: Articulated bones of a mourning dove showing the carpometacarpus and extensor process.

Figure 3. Modified radius of the African Jacana (*Actophilornis africana*).
Modified from Hume & Steel, 2013.

Table 1: Summary of Behavioral Review of Wing-Weaponized Birds										
#	**Common Name**	**Species**	**Family**	**Weapon Type**	**Evidence of Weapon (after Menezes & Palaoro, 2021)**	**Mating System**	**Non-breeding Sociality**	**Space Use**	**Use of Flight**	**Habitat (Billerman, Keeney & Rodewald, 2020)**
1	Egyptian Goose	*Alopochen aegyptiaca*	Anatidae	Knob	Eyton, 1838; Gray, 1849; Delacour & Mayr, 1945; Woolfenden, 1961; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a	Longterm to lifelong monogamous pair bonds (Harrison, 1978c; Kear, 2005)	Winter flocking; may form groups of hundreds or thousands (Maclean, 1997)	Highly aggressive defense of breeding territories (Beazley, 1974; Brown 1982; Milstein, 1993; Satchel & Satchel, 2000; Kear, 2005;)	Sedentary (Carboneras, 1992a)	Africa, wetland and water body
2	Brown Teal	*Anas chlorotis*	Anatidae	Knob	Worthy et al., 1997; Williams, 2015	Monogamous, likely longterm to life-long based on data from closely related or possibly conspecific *A. castanea* (Kear, 2005)	Likely flocking, based on data from closely related or possibly conspecific *A. castanea* (Kear, 2005; Carboneras, Christie & Kirwan, 2020)	Breeding territory defended at least by male (Kear, 2005)	Presumably sedentary (del Hoyo, Collar, Kirwan & Sharpe, 2020)	New Zealand, wetland, water body, coast
3	African Black Duck	*Anas sparsa*	Anatidae	Spur	Chapin, 1932; Phillips, 1932; Kear & Steel, 1971; McKinney et al., 1978; Frost et al., 1979; Livezey, 1991; Kear, 2005; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Multi-year monogamy, however can be only 2 seasons (Kear, 2005)	Breeding pairs remain on territory year round, non-breeding individuals form social flocks (Ball et al., 1978; Kear, 2005)	Pairs vigorously defend territories during breeding season and maintain defence to an extent year round (Ball et al., 1978; Kear, 2005)	Sedentary (Carboneras & Kirwan, 2020a)	Africa, river specialist

4	Greater White-fronted Goose	*Anser albifrons*	Anatidae	Knob	Woolfenden, 1961; Livezey, 1986; Livezey, 1989; Livezey, 1996a; Ericson, 1997; Livezey & Zusi, 2006; Billerman et al., 2020	Longterm monogamy (Boyd, 1953; Ely et al., 2020)	Gregarious winter flocking, but intense physical altercations involving wing slapping may occur (Ely et al., 2020)	Males are territorial while nesting, aggressive interactions are rare. May nest in small groups possibly with more closely related individuals, some degree of cooperative breeding (Fowler, Eadie & Ely, 2004; Ely et al., 2020;)	Highly migratory (Ely et al., 2020)	Far north, migrates to mid-norther or equatorial latitudes, wide range of habitat
5	Canada Goose	*Branta canadensis*	Anatidae	Knob	Swainson & Richardson, 1831; Woolfenden, 1961; Hanson, 1967; Livezey, 1986; Livezey, 1989; Caithamer et al., 1993; Livezey, 1996	Longterm monogamy (MacInnes & Lieff, 1968)	Highly social winter flocking (MacInnes, 1966; Sherwood, 1967; Raveling, 1969b)	Vigorous defense of nesting territory during breeding season, mostly by male (Aldrich, 1983; Carriere, Bromley, Gauthier, 1999)	Highly migratory (Sedinger & Bollinger, 1978)	Migratory range over most of North America, wide range of habitat
6	Cape Barren Goose	*Cereopsis novaehollandiae*	Anatidae	Knob	Latham, 1801; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Livezey, 1996a;	Lifelong monogamy (Kear, 2005)	Flocks form post-breeding seasons (Guiler, 1967)	Pairs vigorously defend breeding territory (Guiler, 1967)	Sedentary (Carboneras & Kirwan, 2020c)	Australia, coastal
7	Kelp Goose	*Chloephaga hybrida*	Anatidae	Knob	Delacour & Mayr, 1945; Rand, 1954; Johnsgard, 1965; Gladstone & Martell, 1968; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Kear, 2005;	Longterm monogamy (Kear, 2005).	Largescale flocking not observed (Carboneras & Kirwan, 2020f)	Pairs defend the same territory and nest site for many contiguous years (Kear, 2005; Liljesthröm et al., 2013)	Sedentary (Kear, 2005)	Southern South America & Falkland Islands, coastal
8	Upland Goose	*Chloephaga picta*	Anatidae	Knob	Delacour & Mayr, 1945; Rand, 1954; Woolfenden; 1961; Johnsgard, 1965; Gladstone & Martell, 1968; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Kear, 2005	Longterm monogamy (Summers & Mcadam, 1993)	Gregarious winter flocking (Todd, 1979, Kear, 2005)	Pairs vigorously defend the same territory each breeding season (Summers & Mcadam, 1993)	Migratory within Southern South America (Kear, 2005)	Southern South America & Falkland Islands, open meadow

9	Ashy-headed goose	*Chloephaga poliocephala*	Anatidae	Knob	Rand, 1954; Livezey, 1986; Livezey, 1996; Delacour & Mayr, 1945; Johnsgard, 1965; Marchant & Higgins, 1990; Livezey, 1989; Livezey, 1996;	Presumably longterm monogamy	Winter flocking (Todd, 1979)	Territory defended at least by male during breeding season (Kear, 2005)	Partially migratory (Kear, 2005)	Southern South America, water bodies or coastal
10	Ruddy-headed Goose	*Chloephaga rubidiceps*	Anatidae	Knob	Delacour & Mayr, 1945; Rand, 1954; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Kear, 2005	Presumably longterm monogamy	Winter flocking (Todd, 1979)	Territory defended at least by male during breeding season (Kear, 2005)	Partially migratory to sedentary (Kear, 2005)	Southern South America & Falkland Islands, open meadow near water
11	Blue-winged Goose	*Cyanochen cyanoptera*	Anatidae	Knob	Delacour & Mayr, 1945; Ruppell, 1845; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b;	Monogamy (Kear, 2005)	Winter flocking (Urban, 1991; Kear, 2005; Ash & Atkins, 2009;)	Highly aggressive territorial defense, dispersed breeding territories (Ripley, 1961)	Sedentary (Kear, 2005)	Africa, meadow near water
12	Blue Duck	*Hymenolaimus malacorhynchos*	Anatidae	Knob	Gray, 1849; Eldridge, 1986b; Livezey, 1986; Woolfenden, 1961; Kear & Steel, 1971; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Kear, 2005; Johnsgard, 2010; Williams, 2015	Monogamy (Triggs et al., 1992)	Pair remains on defended breeding territory (Kear, 2005)	Defense of consistent breeding territory year round, likely for life (Kear, 2005)	Sedentary (Kear, 2005)	New, Zealand, River specialist
13	Torrent duck	*Merganetta armata*	Anatidae	Spur	Gray, 1849; Morgan, 1932; Delacour & Mayr, 1945; Rand, 1954; Woolfended, 1961; Johnsgard, 1966; Weller, 1968; Kear & Steel,1971; Eldridge, 1986a; Livezey, 1986; Madge, 1988; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Kear, 2005; Johnsgard, 2010; Hume & Steele, 2013	Lifelong monogamy (Ippi et al., 2018)	Pair remains on defended breeding territory (Ippi et al., 2018)	Pairs aggressively defend territories year round, both individuals frequently perform aggressive displays toward neighbors (Ippi et al., 2018)	Sedentary, remain on territory near mate for entire life (Ippi, et al., 2018; Eitniear, 2020)	Western South America, River specialist
14	Orinoco Goose	*Oressochen jubatus*	Anatidae	Knob	de Spix, 1825; Gray, 1849; Delacour & Mayr, 1945; Woolfenden, 1961; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Nascimento & Silveira, 2020	Longterm monogamy (Davenport, Endo, & Kriese, 2020)	Small groups observed but typically sighted in pairs year-round (Johnsgard, 1965; Todd, 1979; Davenport, Endo, & Kriese, 2020)	Pairs are highly territorial during breeding season (Johnsgard, 1965; Davenport, Endo, & Kriese, 2020).	Sedentary and predominantly terrestrial (Davenport, Endo, & Kriese, 2020)	South America, near water bodies

15	Andean Goose	*Oressochen melanopterus*	Anatidae	Knob	Delacour & Mayr, 1945; Rand, 1954; Woolfenden, 1961; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a	Presumably longterm monogamy	Presumably similar to Orinocco goose	Pairs defend territory during breeding season (Johnsgard 1965)	Sedentary and predominantly terrestrial (Delacour, 1954)	Andes region of South America, meadow
16	Spur-winged goose	*Plectropterus gambensis*	Anatidae	Spur	Eyton, 1838; Gray, 1849; Sclater, 1886; Lucas, 1893; Phillips, 1922; Chapin, 1932; Morgan, 1932; Rand, 1954; Woolfenden, 1961; Johnsgard, 1965; Livezey, 1986; Halse & Skead, 1983; Livezey, 1989; Livezey, 1989; Zaloumis, 1982; Livezey, 1996a; Livezey, 1996b; Moller, 1992; Marchant & Higgins, 1990; Kear, 2005; Johnsgard, 2010; Hume & Steele, 2013	Little to no aparent pair bond (Brown, Urban, & Newman, 1982; Johnsgard, 2010). Some evidence of aggressive mate gaurding (Johnsgard, 1965)	Winter flocking, large flocks up to tens of thousands (Dowsett, R. J., D. R. Aspinwall, and F. Dowsett-Lemaire, 2008)	Some evidence of males temporarily gaurding nesting sites, males known to be aggressive and somewhat dangerous (Rand, 1954; Brown, Urban & Newman, 1982)	Regional nomadic movements, mostly sedentary (Carboneras & Kirwan, 2020g)	Africa, near water bodies
17	Radjah Shelduck	*Radjah radjah*	Anatidae	Knob	Morgan, 1932; Delacour & Mayr, 1945; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Ericson, 1997	Longterm to life-long monogamy (Kear, 2005)	Winter flocking (Marchant & Higgins, 1990)	Pairs aggressively defend territory during breeding season (Kear, 2005)	Sedentary (Kear, 2005)	Australia & Oceania, coastal
18	Knob-billed Duck	*Sarkidiornis melanotos*	Anatidae	Knob	Eyton, 1838; Gray, 1849; Chapin, 1932; Rand, 1954; Woolfenden, 1961; Livezey, 1986; Livezey, 1989; Marchant & Higgens, 1990; Livezey, 1996a; Livezey, 1996b	Seasonal pair bonds, monogamous to polygynous. Dominance hierarchy within harem females (Brown, Urban, & Newman, 1982; Safford & Hawkins, 2013)	Aggregation in wetland areas during non-breeding season (Gaidet, 2016).	Males establish and defend territory for the entirety of the breeding season to which they attract females (Dallmeier & Cringan, 1989).	Sedentary to somewhat nomadic (Kear, 2005)	Africa and Asia, near water bodies
19	Falkland Steamer Duck	*Tachyeres brachypterus*	Anatidae	Knob	Eyton, 1838; Gray, 1849; Chapin, 1932; Rand, 1954; Woolfenden, 1961; Livezey, 1986; Livezey, 1989; Marchant & Higgens, 1990; Cowles, 1994; Livezey, 1996a; Livezey, 1996b	Longterm to lifelong monogamous pair bonds (Livezey & Humphrey, 1985; Kear, 2005)	Territories are defended by pairs year-round, possibly for life (Livezey & Humphrey, 1985)	Pairs are extremely aggressive in defense of breeding territory against both con- and herterospecifics (Livezey & Humphrey, 1985)	Effectively flightless (Winkler, Billerman, & Lovette, 2020)	Falkland Islands, coastal

2 0	Flying Steamer Duck	*Tachyeres patachonicus*	Anatidae	Knob	Weller, 1976; Livezey & Humphrey, 1984; Neuchterlein & Storer, 1985; Livezey, 1986; Madge, 1988; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Kear, 2005; Hume & Steele, 2013	Longterm to lifelong monogamous pair bonds (Livezey & Humphrey, 1985; Nuechterlein & Storer, 1985; Kear, 2005)	Territories are defended by pairs year-round, possibly for life (Livezey & Humphrey, 1985)	Pairs are extremely aggressive in defense of breeding territory against both con- and herterospecifics (Livezey & Humphrey, 1985; Nuechterlein & Storer, 1985)	Sedentary (Winkler, Billerman, & Lovette, 2020)	Southern South America, water bodies or coastal
2 1	Flightless Steamer Duck	*Tachyeres pteneres*	Anatidae	Knob	Phillips, 1925; Weller, 1976; Livezey & Humphrey, 1984; Neuchterlein & Storer, 1985; Livezey, 1986; Madge, 1988; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Kear, 2005; Hume & Steele, 2013.	Longterm to lifelong monogamous pair bonds (Livezey & Humphrey, 1985; Kear, 2005)	Territories are defended by pairs year-round, possibly for life (Livezey & Humphrey, 1985)	Pairs are extremely aggressive in defense of breeding territory against both con- and herterospecifics (Livezey & Humphrey, 1985)	Effectively flightless (Winkler, Billerman, & Lovette, 2020)	Southern South America, coastal
2 2	South African Shelduck	*Tadorna cana*	Anatidae	Knob	Eyton, 1838; Morgan, 1932; Delacour & Mayr, 1945; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Ericson, 1997	Monogamy (Siegfried; 1976), likely longterm	Non-breeding flocking (Brown, Urban & Newman, 1982)	Pairs aggressively defend territory during breeding season (Taylor, 1944; Ripley, 1961; Geldenhuys, 1980)	Regionally migratory (Allan, 2023)	Southern Africa, near water bodies
2 3	Ruddy Shelduck	*Tadorna ferruginea*	Anatidae	Knob	(Livezey, 1986; Livezey, 1996; Delacour & Mayr, 1945; Johnsgard, 1965; Marchant & Higgins, 1990; Livezey, 1989; Livezey, 1996b; Ericson, 1997; Morgan, 1932	Longterm to life-long monogamy (Zubko, Mezinov, & Popovkina, 2003; Salvador & Amat, 2022)	Winter flocking (Cramp & Simmons, 1977; Hughes & Green, 2005)	Pairs aggressively defend breeding territories, some pairs may defend winter feeding territories (Cramp & Simmons, 1977; Hughes & Green, 2005; Quan & Cui, 2013; Ripley, 1961)	Both migratory and sedentary populations (Salvador & Amat, 2022)	Range including parts of Europe, Asia, and Africa, near wetland

24	Common Shelduck	*Tadorna tadorna*	Anatidae	Knob	Eyton, 1867; Morgan, 1932; Delacour & Mayr, 1945; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Ericson, 1997;	Longterm to life-long monogamy (Pienkowski & Evans, 1982; Kear, 2005)	Winter flocking (Pienkowski & Evans, 1982)	Pairs are extremely aggressive in defense of multi-use breeding territories and/or separate feeding and nesting territories, high site fidelity (Ripley, 1961; Pienkowski & Evans, 1982; Carboneras & Kirwan, 2020d)	Both migratory and sedentary populations (Carboneras & Kirwan, 2020d)	Range including parts of Europe, Asia, and Africa, near wetland or coast
25	Australian Shelduck	*Tadorna tadornoides*	Anatidae	Knob	Morgan, 1932; Delacour & Mayr, 1945; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Ericson, 1997	Longterm monogamy (Kear, 2005)	Winter flocking (Kear, 2005)	Pairs aggressivly defended breeding territory, high site fidelity (Ripley, 1961; Kear, 2005)	Sedentary (Carboneras & Kirwan, 2020b)	Australia, near water bodies
26	Paradise Shelduck	*Tadorna variegata*	Anatidae	Knob	Morgan, 1932; Delacour & Mayr, 1945; Johnsgard, 1965; Livezey, 1986; Livezey, 1989; Marchant & Higgins, 1990; Livezey, 1996a; Livezey, 1996b; Ericson, 1997	Longterm monogamy (Notornis, 2005)	Winter flocking (Notornis, 1979; Kear, 2005)	Pairs aggressively defend breeding territories, high site fidelity (Notornis, 1979; Kear, 2005)	Sedentary (Barker, 1990)	New Zealand, near water bodies
27	Horned Screamer	*Anhima cornuta*	Anhimidae	Double Spur	Gray, 1849; Jeffries, 1881; Lucas,1893; Rand, 1954; Davidson, 1985; Livezey, 1986; Sclater, 1886; Livezey, 1989; Ericson, 1997; Livezey, 1997; Dyke, Gulas & Crowe, 2003; Dyke & Crow, 2008; Hume & Steele, 2013; Billerman et al., 2020; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Long-term monogamy (Naranjo, 1986)	Generally seen in pairs, sometimes small groups or solitary (Naranjo, 1986)	Multi-year defense of feeding and nesting territories, mate-gaurding has been observed (Naranjo, 1986; Barrow, Black & Walter, 1986)	Sedentary, mostly terrestrial (Naranjo, 1986)	South America, near water bodies
28	Southern Screamer	*Chauna torquata*	Anhimidae	Double Spur	Gray, 1849; Sclater, 1886; Lucas, 1893; Morgan, 1932; Rand, 1954; Davidson, 1985; Livezey, 1986; Livezey, 1989; Moller, 1992; Ericson, 1997; Livezey, 1997; Dyke, Gulas, & Crowe, 2003; Kear, 2005; Livezey & Zusi, 2006; Dyke &	Long-term to lifelong monogamy (Stonor, 1939)	Social non-breeding flocks up to 100 birds (Carboneras, 1992b)	Pairs defend breeding territory year round (Stonor, 1939, Carboneras, 1992b)	Sedentary, mostly terrestrial (Carboneras, 1992b)	South America, near water bodies

					Crow, 2008; Ksepka, 2009; Hume & Steele, 2013; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020;					
29	Northern Screamer	*Chauna chavaria*	Anhimidae	Double Spur	Gray, 1849; Sclater, 1886; Lucas, 1893; Morgan, 1932; Rand, 1954; Davidson, 1985; Livezey, 1986; Livezey, 1989; Livezey, 1997; Dyke, Gulas, & Crowe, 2003; Kear, 2005; Dyke & Crowe, 2008; Hume & Steele, 2013; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Long-term monogamy (Kear, 2005)	Observed in pairs or small groups, sometimes singly (Carboneras, Boesman, Kirwan & Sharpe, 2020)	Pairs defend breeding territory year round (Kear, 2005)	Sedentary, (Carboneras, Boesman, Kirwan & Sharpe, 2020)	Northern South America, near water bodies
30	Southern Lapwing	*Vanellus chilensis*	Charadriiae	Spur	Lucas, 1893; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Ward, 1992; Livezey, 2009; Hume & Steele, 2013; Cruz-Bernate, Riascos, & Barreto, 2013; Billerman et al., 2020; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamy, some evidence of possible polyandry (Saracura, Macedo & Blomqvist, 2008; Santos, 2020)	Large flocks in non-breeding season (Saracura, Macedo, & Blomqvist, 2008)	Highly ritualized defense of breeding territories (Santos, 2020)	Sedentary and mostly terrestrial (Santos, 2020)	South America, open grassland, often near water
31	White-headed Lapwing	*Vanellus albiceps*	Charadriiae	Spur	Rand, 1954; Strauch, 1978; Ward, 1992; Livezey, 2009; Hume & Steele, 2013; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamous (Tarboton, 2001)	Flocks in non-breeding season (Dowsett et al., 2008)	Breeding territory aggressively defended against conspecifics (Tarboton, 2001)	Nomadic (Wiersma & Kirwan, 2020f)	South America, riverbanks
32	Masked Lapwing	*Vanellus miles*	Charadriiae	Spur	Smith, 1843; Lucas, 1893; Morgan, 1932; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Ward, 1992; Livezey, 2009; Hume & Steele, 2013; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Longterm monogamy (del Hoyo, Wiersma, Kirwan & Collar, 2020)	Flocks in non-breeding season (del Hoyo, Wiersma, Kirwan & Collar, 2020)	Territorial, faithful to breeding site over time (del Hoyo, Wiersma, Kirwan, & Collar, 2020)	Sedentary to nomadic (del Hoyo, Wiersma, Kirwan, & Collar, 2020)	Australia and New Zealand, open habitat, usually near water
33	Wattled Lapwing	*Vanellus senegallus*	Charadriiae	Spur	Smith, 1843; Rand, 1954; Hayman, Marchant, & Prater, 1986; Strauch, 1978; Ward, 1992; Livezey, 2009; Hume & Steele, 2013; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamous (Urban, Fry & Keith, 1986)	Flocks in non-breeding season (Dowsett-Lemaire, 2006)	Highly territorial against conspecifics (Wiersma, Kirwan & Boesman, 2021)	Sedentary to nomadic (Wiersma, Kirwan & Boesman, 2021)	South America, often near water

34	Spur-winged Lapwing	*Vanellus spinosus*	Charadriiae	Spur	Eyton, 1867; Sclater, 1886; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Moller, 1992; Ward, 1992; Yogev & Yom-tov, 1996; Livezey, 2009; Hume & Steele, 2013; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamous (Urban, Fry & Keith, 1986)	Non-breeding flocks (Wiersma & Kirwan, 2020e)	Aggressively territorial against heterospecifics, but may tolerate conspecifics. Territories sometimes maintained year-round (Wiersma & Kirwan, 2020)	Sedentary to nomadic (Wiersma & Kirwan, 2020e)	Africa and Middle East, open habitat near water
35	Blacksmith Lapwing	*Vanellus armatus*	Charadriiae	Spur	Sclater, 1886; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Nixon, 1987; Ward, 1992; Tree, 1999; Livezey, 2009; Hume & Steele, 2013; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamous (Wiersma, Kirwan & Boesman, 2020)	Large non-breeding flocks (Tree, 1998)	Defends breeding territory but intraspecific aggression rarely occurs (Wiersma, Kirwan & Boesman, 2020)	Sedentary (Wiersma, Kirwan, & Boesman, 2020)	Southern Africa, open habitat near water
36	River Lapwing	*Vanellus duvaucelii*	Charadriiae	Spur	Sclater, 1886; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Ward, 1992; Livezey, 2009; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Presumably monogamous (Duckworth, Timmins, & Evans, 1998)	Generally solitary or paired, small groups may occur (Wells, 1999)	Defends breeding territory (Duckworth, Timmins, & Evans, 1998; Mishra, Kumar, & Kumar, 2021)	Sedentary to nomadic (Wiersma & Kirwan, 2020d)	Asia, near water
37	Pied Lapwing	*Vanellus cayanus*	Charadriiae	Spur	Sclater, 1886; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Livezey, 2009	Little data available	Flocking observed (Olmos, 1993)	Little data available	Sedentary, possibly nomadic (Ridgely & Greenfield, 2001)	South America, near water bodies or coastal
38	Long-toed Lapwing	*Vanellus crassirostris*	Charadriiae	Spur	Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Ward, 1992; Livezey, 2009; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamous (Wiersma & Kirwan, 2020b)	Frequentyl solitary, may be found in pairs or groups (Urban, Fry, & Keith, 1986; Dowsett-Lemaire, 2006)	Small breeding territory, very aggrssively defended against conspecifics and heterospecifics (Walters, 1979; Urban, Fry & Keith, 1986)	Sedentary to nomadic (Wiersma & Kirwan, 2020b)	Africa, wetlands

39	Yellow-wattled lapwing	*Vanellus malabaricus*	Charadriiae	Spur	Sclater, 1886; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Ward, 1992; Livezey, 2009; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamous (Hayman, Marchant, & Prater, 1986)	Small family groups or flocks (Hayman, Marchant, & Prater, 1986)	Large breeding territories aggressively defended by pairs (Hayman, Marchant, & Prater, 1986)	Sedentary (Dissanayake et al., 2014)	South Asia, open habitats
40	Andean Lapwing	*Vanellus resplendens*	Charadriiae	Spur	Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Ward, 1992; Livezey, 2009; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Monogamous (Dillensager et al., 2022)	Small flocks occasionally observed (Dillensager et al., 2022)	Pairs aggressively defend territories against conspecifics and hetreospecifics (Dillensager et al., 2022)	Sedentary (Schulenberg, et al., 2007)	Andes region of South America, meadow and marsh
41	Gray-headed Lapwing	*Vanellus cinereus*	Charadriiae	Spur	Rand, 1954; Hayman, Marchant, & Prater, 1986; Strauch, 1978; Ward, 1992; Wakisaka et al., 2006; Livezey, 2009	Monogamous (Wiersma & Kirwan, 2020a)	Non-breeding flocks (Wiersma & Kirwan, 2020a)	Defends breeding territories (Wiersma & Kirwan, 2020a)	Most populations are migratory, some sedentary (Wiersma & Kirwan, 2020a)	Asia, wetland or water body
42	Red-wattled Lapwing	*Vanellus indicus*	Charadriiae	Spur	Rand, 1954; Strauch, 1978; Ward, 1992; Livezey, 2009	Monogamous (Wiersma & Kirwan, 2020c)	Flocks observed (Noor et al, 2018)	Pairs defend breeding territories, known to show site fidelity over seasons (Muralidhar & Barve, 2013; Wiersma & Kirwan, 2020c)	Likely primarily sedentary (Wiersma & Kirwan, 2020c)	South Asia and Middle East, open habitat near water
43	Snowy Sheathbill	*Chionis albus*	Chionidae	Spur	Gray, 1849; Strauch, 1978; Davidson, 1985; Moller, 1992; Forster, 1996; Livezey & Zusi, 2006; Livezey, 2009; Hume & Steele, 2013	Longterm monogamy (Parmalee, 1992; Forster, 1996)	Relatively social unless feeding competition occurs (Murphy, 1936)	Pair aggressively defends breeding territory, male more active. High site fidelity (Forster, 1996)	Migratory between Southern South America and Antarctic islands (Fang, 2020)	Southern South America and Antarctic islands, coastal
44	Black-faced Sheathbill	*Chionis minor*	Chionidae	Spur	Gray, 1849; Burger, 1980; Davidson, 1985; Livezey, 2009	Multi-year Monogamous (Jouventin, Bried, & Ausilio, 1996)	Unclear, non-breeding birds known to be slightly less sedentary than breeders (Jouventin, Bried & Ausilio, 1996)	Pairs defend breeding territories, sometimes year-round (Jouventin, Bried, & Ausilio, 1996)	Sedentary (Bried & Jouventin, 1997)	Prince Edward and adjacent islands, coastal

45	Tooth-billed Pigeon	*Didunculus strigirostris*	Columbidae	Knob	Lucas, 1893; Sclater, 1886; Elliot, 1888; Fisher, 1940; Rand, 1954; Strauch, 1978; Davidson, 1985; Hayman, Marchant, & Prater, 1986; Moller, 1992; Livezey, 2009; Lipshutz, 2017; Billerman et al., 2020; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Little data available	Now typically sighted solitarily, previously recorded in flocks (Gibbs, Barnes, & Cox, 2001)	Little data available	Mostly terrestrial, presumably sedentary (Serra et al., 2018; Baptista &… Sharpe et al., 2020)	Samoa, limited habitat
46	Western Crowned Pigeon	*Goura cristata*	Columbidae	Knob	Morgan, 1932; Worthy, 2001; Livezey & Zusi, 2006; Hume & Steele, 2013; Classens & Meijer, 2015	Little data available	Gregarious (Beehler, Pratt & Zimmerman, 1986).	Aggressive activity including wing raising displays known to occur, but context unclear (Goodwin, 1983)	Sedentary, mostly terrestrial (Goodwin, 1983; Baptista &…Bonan et al., 2020)	New Guinea, rainforest, marsh, mangrove
47	Wattled Jacana	*Jacana jacana*	Jacanidae	Spur	Elliot, 1888; Sclater, 1886; Lucas, 1893; Rand, 1954; Elliot, 1978; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Emlen & Wrege, 2004; Livezey & Zusi, 2006; Livezey, 2009; Lipshutz, 2017; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Polyandrous (Emlen, Wrege, & Webster, 1998)	Non-breding birds form flocks (McCrary et al., 2009)	Females defend territories encompassing smaller defended territories of multiple males. Year round defense in some areas. Aggression is intense and many non-territorial individuals are excluded from breeding (Emlen, Wrege, & Webster, 1998; Pacheco & Piratelli, 2005)	Sedentary to nomadic (McCrary et al., 2009)	South America, wetland

48	Northern Jacana	*Jacana spinosa*	Jacanidae	Spur	(del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020; Billerman et al., 2020; Hayman, Marchant, & Prater, 1986; Lipshutz, 2017; 164, Strauch, 1978; Rand, 1954; Davidson, 1985; Lucas, 1893; Elliot, 1888; Livezey, 2009; Sclater, 1886; Moller, 1992	Polyandrous (Jenni & Collier, 1972)	Non-breeding birds form flocks (Jenni & Mace, 2020)	Females defend territories encompassing smaller defended territories of multiple males. Highly aggressive, females may defeat and take full harems from other females. Territoriality may be year round, many non-territorial birds are excluded from breeding (Jenni & Collier, 1972; Jenni & Mace, 2020)	Sedentary, weak flyer (Howell & Webb, 1995; Jenni & Mace, 2020)	Central America and Carribean, wetland
49	Pheasant-tailed Jacana	*Hydrophasianus chirurgus*	Jacanidae	Spur	Elliot, 1888; Lucas, 1893; Rand, 1954; Strauch, 1978; Davidson, 1985; Hayman, Marchant, & Prater, 1986; Livezey, 2009; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Polyandrous (Jenni & Kirwan, 2020d)	May forage in loose groups (Ramachandran, 1998)	Females defend territories encompassing smaller defended territories of multiple males (Wells, 1999; Jenni & Kirwan, 2020d)	Nomadic to regionally migratory, only Jacana with any type of migratory movement (Jenni & Kirwan, 2020d)	Asia, Oceania, wetland
50	African Jacana	*Actophilornis africana*	Jacanidae	Knob; Weaponized Radius	Elliot, 1888; Lucas, 1893; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Livezey, 2009	Typically polyandrous (Dowsett-Lamaire & Dowsett, 2014; Jenni & Kirwan, 2020a)	Non-breeding birds form flocks (Gatter, 1997; Ash & Atkins, 2009; Dowsett-Lamaire & Dowsett, 2014)	Females defend territories encompassing smaller defended territories of multiple males (Dowsett-Lamaire & Dowsett, 2014; Jenni & Kirwan, 2020a)	Highly nomadic (Gatter, 1997; Ash & Atkins, 2009; Dowsett-Lamaire & Dowsett, 2014)	Africa, wetland
51	Madagascar Jacana	*Actophilornis albinucha*	Jacanidae	Knob; Weaponized Radius	Saint-Hillaire, 1832; Lucas, 1893; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Livezey, 2009	Little data, but likely polyandrous (Jenni & Kirwan, 2020c)	Typically single or paired, may form large groups (Safford	Little data, but likely similar to *A. africanus* (Jenni & Kirwan, 2020c)	Sedentary to nomadic (Safford & Hawkins, 2013)	Africa, wetland

							& Hawkins, 2013)			
52	Bronze winged Jacana	*Metopidius indicus*	Jacanidae	Knob; Weaponized Radius	Elliot, 1888; Lucas, 1893; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Livezey, 2009; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Polyandrous (Butchart, Seddon & Ekstrom, 1999; Butchart, 2000)	Seem not to form cohesive flocks (Butchart, 2000)	Females defend territories encompassing smaller defended territories of multiple males (Ekstrom, 1999; Butchart, 2000; Butchart, Seddon)	Sedentary to nomadic (Spierenburg, 2005)	Asia, wetland
53	Comb crested Jacana	*Irediparra gallinacea*	Jacanidae	Knob; Weaponized Radius	Elliot, 1888; Lucas, 1893; Rand, 1954; Strauch, 1978; Hayman, Marchant, & Prater, 1986; Livezey, 2009; del Hoyo, Elliot, Sargatal, Christie, & de Juana, 2020	Polyandrous (Mace, 2000)	Non-breeders may flock (Favaloro, 1931)	Females defend territories encompassing smaller defended territories of multiple males. May hold territory year-round (van Balen & Prentice, 1997; Mace, 2000)	Sedentary (Dostine & Morton, 2000)	Australia/Oceania, wetland
54	Coscoroba Swan	*Coscoroba coscoroba*	Anatidae	Almost certain lack of weaponry	Lucas, 1893; Livezey, 1986; Livezey, 1989; Livezey, 1996a	Longterm monogamy (Kear, 2005)	Non-breeding flocks (Kear, 2005)	Aggressively defend breeding territories, occasionally year round (Silva Garcia & Brewer, 2007)	Regionally migratory (Kear, 2005)	South America, wetland or water bodies
55	Freckled Duck	*Stictonetta naevosa*	Anatidae	Almost certain lack of weaponry	Livezey, 1986; Livezey, 1989; Livezey, 1996a; Ericson, 1997	Presumably monogamous (Marchant & Higgins, 1990; Carboneras & Kirwan, 2020e)	Non-breeding flocks (Johnsgard, 2010)	Nest gaurded by male, but not observed to be particularly aggressive or territorial (Marchant & Higgins, 1990; Carboneras & Kirwan, 2020e)	Sedentary to nomadic (Kear, 2005)	Australia, water bodies

56	White-backed Duck	*Thalassornis leuconotus*	Anatidae	Almost certain lack of weaponry	Livezey, 1986; Livezey, 1989; Ericson, 1997	Monogamous (Kear, 2005)	Non-breeding flocks (Kear, 2005)	Not territorial (Kear, 2005)	Sedentary to nomadic (Kear, 2005)	Africa, water bodies

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Chapter 2:

Not So Peaceful:

Investigating Skeletal Weaponization

in Two *Zenaida* Doves

Abstract

The white-winged dove and the mourning dove are two closely related North American Columbid species that display aggressive wing-slapping behavior. This behavior, observed in several avian families, is sometimes accompanied by weaponizing osteological modifications to the carpometacarpus bone. I hypothesized the existence of such weapons in white-winged and mourning doves due to their common use of wing-slapping. To explore this hypothesis, I made two predictions based on patterns of modification in birds with well documented weaponry. I predicted that, if weaponry exists in these birds, 1) white-winged doves will show greater weaponization than mourning doves, and 2) males of each species will show greater weaponization than females. To test these predictions, I collected wing bones from 38 doves and analyzed 19 linear measures of each wing. There was no significant difference in bone size or shape between species, and no significant sexual dimorphism in mourning doves. However, in white-winged doves, there was significant sexual dimorphism in the height of the carpometacarpal extensor process, a feature that is commonly modified in weapon-bearing birds. This finding is consistent with the hypothesis that white-winged doves possess weaponizing bone modifications. Possibilities for further study of possible weaponry in white-winged doves are explored.

Introduction

Doves are a symbol of peace and love, easily recognized in literature, religion, and in evolutionary game theory, but this symbolism is a bit misplaced. Columbidae, the family encompassing pigeons and doves, may deserve a more violent reputation. Among ornithologists and pigeon aficionados, members of this family are noted for an interesting form of aggression: fighting with their wings (Johnston, 1960; Harrison, 1961; Goodwin, 1983; Swanson & Rappole, 1993; Murton & Isaacson, 2008; Johnson & Donaldson-Fortier, 2009; Fronimos, et al., 2011; Mohamed et al., 2016). Although birds in the Columbidae family do utilize other aggressive behaviors, slapping with the wing is a common method of attack and defense across this family (Luccas, 1893; Goodwin, 1983). Wing-slapping is commonly used to define aggressive behavior in neurobiological studies of Columbids (Cross & Goodman, 1988; Buntin, 1991; Fachinelli et al., 1996; Goldberg et al., 2001; Mohamed et al., 2016). Despite the often-noted instances of this behavior in literature, it has not frequently been the focus of study.

The use of wings during aggressive interactions is not limited to Columbidae. This behavior is observed in other families, including waterfowl (*Anatidae*), jacanas (*Jacanidae*), and lapwings (*Charadriidae*)(See Ch. 1, Table 1). This odd form of aggression is often associated with weaponizing modifications to the bone morphology of the wings. There are 53 wing-slapping avian species with well documented osteological wing weaponry, and upwards of 70 others in which modification is strongly indicated (Menezes & Palaoro, 2021). The majority of such weapons occur as a modification of a bony process near the 'wrist' of the bird, specifically, on the carpometacarpus bone (Fig.1) (Rand, 1954; Menezes & Palaoro, 2022). The carpometacarpus is a fusion of carpal and metacarpal bones that supports the portion of a bird's wing distal to the carpal joint (i.e., the joint that separates primary from secondary feathers). A projection near the proximal end of this bone, termed the extensor process, serves as an attachment point for extensor muscles in the wing, and for the ligaments supporting the patagial membrane of the extended wing. This process has, in several different avian clades, been co-opted as a weapon. In addition to the more obvious modifications to the carpometacarpal extensor process, shortening and thickening of wing bones is observed in some weapon-bearing species, possibly to provide structural support and reduce the possibility of bone damage when wing-slapping occurs (Livezey & Humphrey, 1984; Longrich & Olson, 2011; Hume & Steel, 2013).

There are two main forms of weaponization that occur in wing-slapping birds: wing spurs and wing knobs. Wing spurs are arguably the more noticeable of the two modification types, and knobs have occasionally been referred to as rudimentary spurs, particularly in early literature (Morgan, 1932; Rand, 1954). Spurs appear as sharp protrusions, taller than they are wide. Each spur is comprised of a boney core covered in an external cornified sheath (Rand, 1954; Stettenheim, 2000)(Fig. 2). Conical or pyramidal in shape, spurs are reminiscent of a spear or blade, and often contrast in color with wing plumage (Fig. 3). Spurs are well documented in all screamers (*Anhimidae*) and sheathbills (*Chionidae*), several jacanas (*Jacanadae*) and lapwings (*charadriidae*), as well as a few species of waterfowl (*Anatidae*)(See Ch. 1, Table 1)(Menezes & Palaoro, 2022). Although most wing spurs occur as modifications of the extensor process of the carpometacarpus, this is not always the case. *Anhimidae* species possess two spurs, one of which is a modification of the extensor process, and the other of which occurs at the distal end of the carpometacarpus (Rand, 1954). The spur-winged goose *(Plectropterus gambensis*) displays a wing spur as a modification of the radial carpal bone (Rand, 1954). However, these atypical spur locations are thought to be unique to these birds (Menezes & Palaoro, 2021).

In contrast to wing spurs, all known wing knobs occur on the extensor process of the carpometacarpus. These structures, like spurs, are underlain by a bony expansion of this process, but often do not have an obvious external cornified component. The expansion of the process is typically more globular in shape than a spur, and functions like a club (Nuechterlein & Storer, 1985; Hume & Steel, 2013). Carpal knobs occur in many waterfowl (*Anatidae*), several jacanas (*Jacanadae*) and have been described among a few species of pigeons and doves (*Columbidae*)(Billerman et al., 2020; Ch. 1 Table 1). Among the crowned-pigeons (*Goura*), all three species possess small boney outgrowths of the carpometacarpal extensor process, but they are best documented in the western crowned pigeon (*Goura cristata*) (Worthy, 2001; Hume & Steel, 2013; Menezes & Palaoro, 2021)(Fig. 4). The tooth-billed pigeon (*Didunculus strigirostris)*, the only extant member of *Didunculus*, has long been noted to have an external cornified knob, but some osteological studies indicate a lack of noticeable skeletal modification in this bird (Lucas, 1893; Morgan, 1932; Rand, 1954; Livezey, 1993; Worthy & Wragg, 2008). Some extinct Columbids, including the Viti Levu giant pigeon (*Natunaornis gigoura*) and the Rodrigues Island solitaire (*Pezophaps solitaria*), also possess carpal knobs (Worthy, 2001; Hume & Steel, 2013). Solitaire fossils have the most extreme examples of carpal knobs known in any bird, sometimes greater than 2 cm in length, that were originally described as ‘musket balls’ (Fig. 5) (Hume & Steel, 2013). The solitaire also provides an example of shortening and thickening of wing bones sometimes associated with weaponization, in addition to moderate inflation of the radius and ulna (Hume & Steel, 2013).

Evidence of bony weaponry, including both wing weapons and tarsal weapons, has been documented in less than two percent of bird species. While in-depth study of behavioral and ecological factors associated with the existence of these weapons is lacking, some contextual patterns for weaponization do appear (see Ch 1. Summary). For example, wing weapons are frequently sexually dimorphic. Although wing weaponry is present in both sexes of many species, such modifications are usually more pronounced in males, who typically participate more in territorial defense (Rand, 1954; Frost et al., 1979; Wakisaka et al., 2006; Hume & Steel, 2013; Williams & Road, 2015; Meissner et al., 2021). As an exception, among the sex-role-reversed jacanas, females have proportionally larger spurs than males (Emlen & Wrege, 2004; Davidson, 2009). Additionally, weaponization is often more pronounced in groups with greater potential or necessity for aggressive intraspecific competition. Species with wing weaponry typically display very aggressive defense of nesting habitat or resources (including mates). In parallel, wing-slapping in Columbids appears to be used primarily in defense of nesting territory or food sources (Johnston, 1960; Harrison, 1961; Swanson & Rappole, 1993; Murton & Isaacson, 2008; Johnson & Donaldson-Fortier, 2009; Fronimos, et al., 2011; Mohamed et al., 2016). Within Anatids, the avian family with the most documented instances of wing weaponry, some of the most pronounced carpal weapons occur in species where resources or habitats are highly specialized and thus highly contested. For example, the torrent duck pairs (*Merganetta armata*), a species with one of the more pronounced examples of wing weaponry among Anatids, are river specialist ducks that defend narrow, linear territories along fast-flowing mountain rivers (Ch 1., Table 1.13). Such territories are limited and highly contested, and non-territorial individuals lack breeding opportunities (Ippi et al., 2018). Similar patterns appear in several other river specialist ducks, which are also weapon-bearing (Ch 1. Table 1.3, 1.12).

My objective in this study was to explore the presence of weaponizing modifications in Columbid species where the possibility of weaponization remains unstudied. Although phylogenetic relationships within Columbidae are not fully resolved, modern work consistently places the known weapon-bearing Columbids (i.e, *Goura, Didunculus, Pezophaps,* and *Natunaornis)* within an Indo-Pacific sub-family (Worthy, 2001; Shapiro et al., 2002; Pereira et al., 2007; Soares et al., 2016). Little research has explored possible wing weaponization in New-World Columbid clades (Menezes and Palaoro, 2021). This is surprising considering the frequently noted observations of wing-slapping behavior among feral rock doves and North American doves. Two species of Columbids, the white-winged dove (*Zenaida asiatica*) and the mourning dove (*Zenaida macroura*), were used in this study. These two *Zenaida* species are common backyard birds in the southwest United States, and both have been observed to use wing-slapping behaviors in defense of the nest and food sources (Irby, 1927; Swanson & Rappole, 1993; Fronimos et al., 2011; T.G. Murphy, pers. comm; Author pers. observation). In this study, I test the hypothesis that white-winged doves and mourning doves display evidence of osteological modifications associated with their wing-slapping behavior. I explore two different predictions, based on patterns observed in other weapon-bearing bird species. First, I predict more pronounced weaponizing modifications among dove species with the greater likelihood of nest site competition, and defense against conspecifics. Specifically, I predict that the colonially nesting white-winged dove will have greater weaponization than the mourning dove, a more dispersed nester. Notably, aggressive interactions among white-winged doves have been observed to increase with colony density (Swanson & Rappole, 1993). Secondly, I predict the presence of sexual dimorphism in osteological weaponization, with males of both species showing greater modification.

Methods

To test the relationships between species, sex, and bone morphology, I compared wing bones of adult white-winged (abbr. WWDO; *Zenaida asiatica*) and mourning doves (abbr. MODO; *Zenaida macroura*). I collected linear measurements and shape ratios of wing bones, and corrected comparisons for differences in individual body-size (see below). Dove carcasses were donated by San Antonio-area hunters. Adult birds were identified using molt/plumage coloration, gonad size, and soft part coloration. A multi-trait approach was used to determine bird age due to the near-year-round breeding of doves in Texas and the poor state of some specimens due to shooting, transportation, freezing, and thawing. Birds of either species displaying any juvenile traits (i.e., buff-colored tips on coverts, lack of iridescence, dull coloration of eye-ring etc.) were classified as juvenile birds and were excluded from the study. Among white-winged doves, dull pink or brown foot coloration and lack of vibrant orange iris were also considered juvenile traits (Ridgeway, 1916; Riddle, 1928; Petrides, 1950; Wight et al., 1967; Wood, 1969; Baskett et al., Oberholser, 1974; 1993; George et al., 1994; Fedynich & Hewitt, 2009).

Individual birds were included in the study only when age and sex could be determined and all skeletal components of both wings and at least one foot were intact. Wings and tarsus were de-feathered and dermestid beetles were used to remove the soft tissue before measurement.

A total of nineteen linear measurements were taken of the wing of each bird. No significant difference in bone measures collected from a subset of right versus left wings were found (Wilcoxon signed rank test, N=6-18, $P < 0.05$ in all tests) therefore only the right wing bones were used in all analyses. Additionally, the length of the tarsometatarsus (ankle bone) of each bird was measured as a proxy for body size to be used in statistical analyses. Measurement repeatability for all measures was found to be high using the rptR R package ($R > 0.8$) (Stoffel et al., 2017; following Lessels & Boag, 1987). All measurements were taken to one hundredth of a millimeter using digital calipers. Because the extensor process of the carpometacarpus has been found to be the primary location of weaponizing modification in wing-slapping birds (Rand, 1954; Menezes & Palaoro, 2021), five measurements of the extensor process were collected. These measurements included: a) length from behind the *process alularis* to the distal tip of the extensor process, b) height across the bone from the *facies articularis ulnocarpalis* to the distal tip of the extensor process, c) width of the process base in the dorsoventral plane, d) and right-angle widths of the process tip in the dorsoventral plane and e) the mediolateral plane (Fig. 6). To explore the potential shortening and thickening of wing bones that sometimes accompanies wing weaponization (Livezey & Humphrey, 1984; Longrich & Olson, 2011; Hume & Steel, 2013), the greatest length for the four major wing bones (humerus, radius, ulna, and carpometacarpus), and midpoint widths of these four bones in the dorsoventral and the anterior-posterior planes, were also collected. Right-angle width measurements were taken for both the major and minor digit of the carpometacarpus. In addition to linear measurements, ratios between the two right-angle width measures of each major wing bone as well as the right-angle measures of the extensor process tip were calculated to provide a representation of bone shaft shape (roundness).

Statistical Methods

I compared differences between linear measures and shape ratios in two main categories: the extensor process shape and size, and major bone shape and size. To compare linear bone measurements between species, the measurements of both species within a sex were regressed against the tarsometatarsus bone. This regression provided a general scaling pattern within a sex, across species, for each linear measure. To investigate differences in scaling between species, a student's t-test was conducted to compare residuals of each wing measure within each sex (thus I tested species bone differences separately between males and females). To test for weaponization differences between the sexes within each species, a backwards stepwise multiple regression was performed that included both body size and sex as predictors of wing bone linear measures. Body size was removed from the model when not significantly related to a linear measure. For each of the two predictions (1: WWDO vs MODO, 2: and male vs female within each species), each set of shape ratios were analyzed using a student's t-test. Shape ratios of major bone shafts were computed by dividing the dorsoventral midpoint width by the anterior-posterior midpoint width. Extensor process tip shape was computed by dividing the dorsoventral tip width by the mediolateral tip width. As these measurements represented shape ratios of structures within the same wing, no body-size standardization was necessary. All statistical analyses were conducted using JMP (JMP 16.1, SAS Institute Inc.). Final sample size for this study included 10 male and 10 female white-winged doves, and 9 male and 9 female mourning doves. Due to the number of analyses contributing to conclusions in each category (potential weaponization of extensor process morphology, and potential supporting structures of wing bones), Bonferroni corrections were applied to alpha values. Bonferroni corrections result in a modified alpha value of 0.003 for 19 major bone shape and size comparisons per prediction and a modified alpha value of 0.008 for 6 extensor process shape and size comparisons per prediction.

Results

Full statistical results are reported in Appendix 1. Between-species comparisons indicate no significant differences in bone shape or size between white-winged and mourning doves of either sex. Specifically, there were no significant differences between species in the greatest lengths, linear midpoint widths, or midpoint shape ratios of major wing bones (Table 1; Table 2). There was also no significant difference between species in any extensor process linear measurement or in extensor process tip shape (Table 1; Table 2). For sexual dimorphism comparisons in mourning doves, there were no significant differences in bone size or shape (Table 3; Table 4; Table 5). Among white-winged doves, there was a significant difference between sexes in the extensor process height from the *facies articularis ulnocarpalis* to the distal tip of the extensor process ($F(1,18) = 3.5877$, $p = 0.002$) (Fig. 7). Other comparisons of sexual dimorphism in white-winged doves were not significant (Table 3; Table 4; Table 5).

Discussion

In order to assess whether two species of wing-slapping new-world doves possess weaponizing modifications to support this unusual agonistic behavior, I compared species differences, as well as sexual dimorphism, in wing osteology. Specifically, I tested the predictions that the colonially-nesting white-winged dove would have greater osteological evidence of weaponization than the mourning dove, and that in both species, males would have greater weaponization than females. I did not find significant differences in between-species analyses. However, my results indicate that there is sexual dimorphism in the height of the extensor process among white-winged doves. Sexual dimorphism in this measure is highly informative, as the same measure has been used in-and-of-itself to compare osteological modification among other weaponized avian species (Williams & Road, 2015). Additionally, the sexual dimorphism in extensor process height is detected only in white-winged doves, the species I predicted would have greater weaponization. As such, despite not finding a difference in osteological weaponization in our between-species analysis, this observation also provides incidental support for our hypothesis through prediction one.

Although these findings are consistent with weaponizing modification, I am hesitant to claim that these results alone are sufficient to define osteological wing weaponry in white-winged doves. The modification described here is quite subdued compared to many well-known examples in weapon-bearing birds. However, subdued weaponry in white-winged doves may be consistent with recent literature in the field of avian weaponry. Menezes and Palaoro (2022) conducted a large scale analysis of wing-weaponization across avian taxa and concluded that weaponization is selected against in highly volant species, including those that display frequent intense flight (as in hummingbirds) and those that display long-term sustained flight (as in long-distance migrators). Energetic and phylogenetic analyses support the conclusion that the additional weight of bony weapons may be disadvantageous to birds with life history and behavioral strategies that are highly dependent on time spent flying (Menezes and Palaoro, 2022). Additionally, the findings of Menezes and Palaoro (2022) provide evidence that larger birds are less affected by this cost, likely due to their increased efficiency in converting metabolic work into mechanical work in flight (Ward et al., 2001; Videler, 2005; Guigueno et al., 2019; Menezes & Palaoro 2021; Menezes & Palaoro, 2022).

While the migratory patterns and sizes of white-winged and mourning doves are not enormously different, it is interesting to speculate about the effects that these factors might have on weaponization in these species. The mourning dove is generally a longer-distance migrant compared to the white-winged dove and is also a smaller species (Otis et al. 2020; Schwerter et al., 2020). Migration, particularly in certain mourning dove populations that may travel thousands of miles, paired with the comparatively small body size of the mourning dove, may result in greater selective pressure against highly developed wing weapons in mourning doves than in white-winged doves. However, white-winged doves are also relatively small migratory birds on which these pressures undoubtedly act, yet the findings of this study indicate osteological modification consistent with weaponization in white-winged doves. These results suggest that despite the selective pressure against weapon development among migrating species, we may yet discover subdued forms of weaponizing carpal modification in North American Columbid species, particularly those with comparatively short-distance migration and larger body size.

A more well-rounded, ecologically based understanding of wing-slapping behavior and associated weaponization is particularly relevant for our species of interest for two reasons. First, the range of the white-wing dove has expanded northward significantly in the last several decades (Schwertner et al., 2020). This species, once found no farther south than the Rio Grande Valley, is now commonly seen as far north as Oklahoma, and occasionally into Canada (Schwertner, et al., 2020). This range expansion has brought white-winged doves into contact with populations of mourning doves with which they have not previously interacted. There is some concern about competition between white-winged and mourning doves, and the apparent incursion of white-winged doves into Texas urban areas, where they seem to have largely replaced mourning doves based on anecdotal reports. Understanding the potential factors affecting outcomes of aggressive competition between these species is important for predicting how white-winged dove range expansion may affect mourning dove range in the future.

Secondarily, it is important to gain understanding of wing-slapping in an ecological context to understand aggressive interactions that may occur between native Texas doves and the invasive Eurasian collared dove, a large, aggressive species which is also known to display wing-slapping behavior (Johnson & Donaldson-Fortier, 2009). There are many questions that remain surrounding the use of wing-slapping behavior and weaponry in white-winged and mourning doves. With how much force can these birds actually strike? In what contexts is wing-slapping used rather than biting or pecking? Does the white-wing dove truly participate in more frequent wing-slapping as a result of its colonial nesting behavior? Answering such questions will create a better understanding of the social interactions of Texas doves, and of wing weaponry as a phenomenon in Aves.

Detecting subdued wing weaponization in Columbids, or other under-explored taxa, will likely require more advanced techniques than those available for this initial study. For example, micro-CT scanning could provide higher precision than caliper measurements and would allow for cross-sectional analysis of bones, which would provide more opportunities to explore bone shape. Furthermore, this technique would provide an opportunity to explore the possibility of increased bone density, a structural feature sometimes associated with weaponization, which I was unable to investigate in this study (Longrich & Olson, 2011; Hume & Steel, 2013). The precision of micro-CT scanning would also allow for analysis of the smaller bones of juvenile birds, which can be difficult to measure with high consistency using calipers. Investigation of juvenile weapons may prove fruitful, as development of weaponizing structures throughout a bird's lifetime is not well understood in most species. There is evidence of consistent spur growth over time in some species, and of weapons being present in juvenile birds, but it has also been proposed that the growth of some knobs may be a plastic change resulting from the repeated stress of wing-slapping by adult birds (Rand, 1954; Hume & Steel, 2013; del Hoyo, 2020). Better understanding of the ontogeny of wing weapons - how they first develop, and how they change over time - could provide important insights toward identifying the presence of subdued weaponry. Exploration of the genetic processes that lead to the development of weapons in some species and not others could be similarly helpful. There is much work to be done to determine what evidence might convincingly support an observation that a subdued carpal modification is, in fact, a weapon.

As it stands, our understanding of weaponry in birds is surprisingly limited. Despite birds being heavily represented in ecological research, mentions of wing weaponry are conspicuously meagre in reviews of weaponry and associated behavior. Nonetheless, patterns that can be gleaned from existing research on the ecology of weapon-bearing birds allow us to make predictions about when avian weaponry will evolve. Using such predictions, I have presented evidence that white-winged doves display significant, although subdued, sexual dimorphism in the height of the extensor process of the carpometacarpus, which is consistent with weaponizing modifications found in other birds. It is my hope that this finding inspires further exploration of the possibility of weaponry in white-winged doves, and in other species where the weaponry has been under-explored. There are many questions left to answer if we are to understand avian weaponry, but as my findings here have shown, we can move toward those answers even by working with the birds we find in our backyards.

Appendix 1: Figures

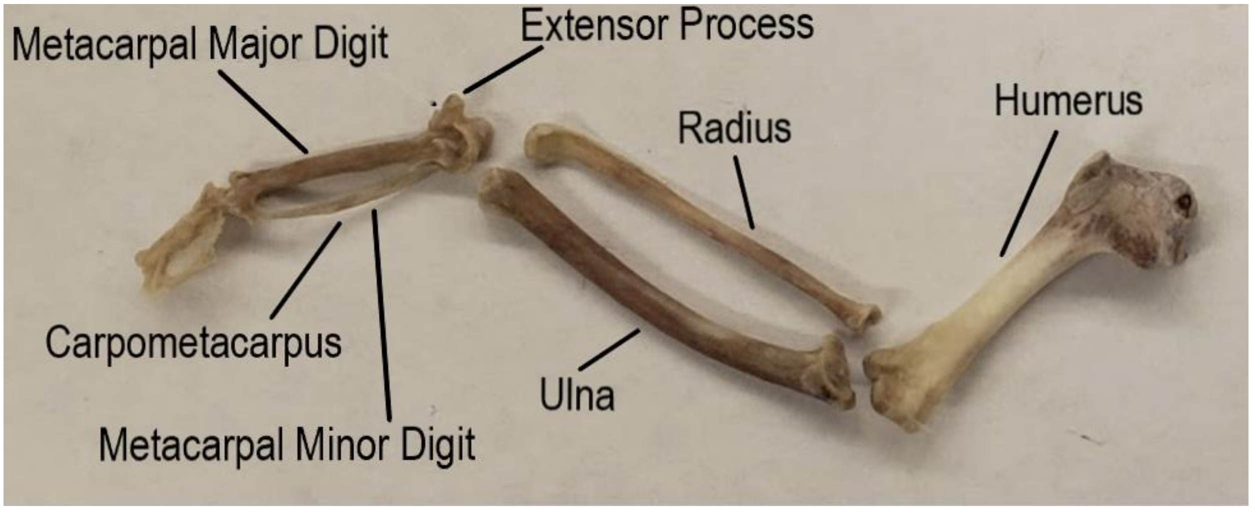

Figure 1: Articulated mourning dove wing bones showing the structures of interest for this study.

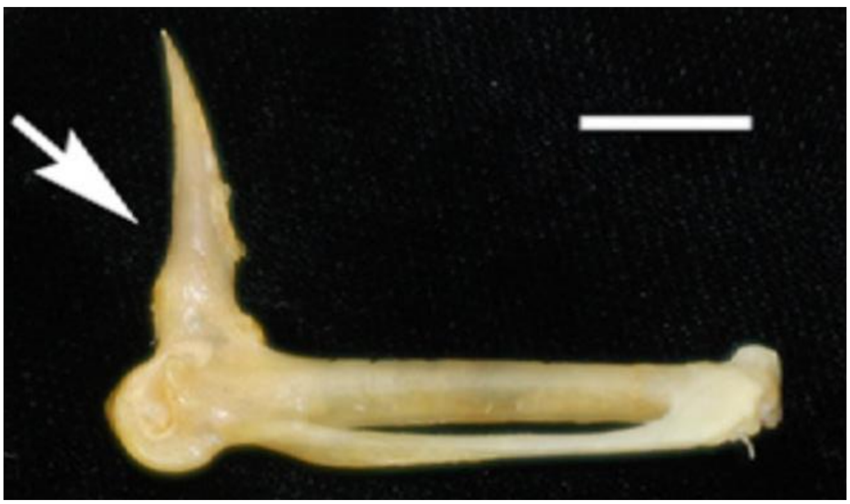
Figure 2: Carpal spur of the masked lapwing (*Vanellus novaehollandiae*).
Modified from Hume & Steel, 2013.

Figure 3: An example of prominent wing spurs near the carpal joint of the southern lapwing (*Vanellus chilensis*). Photo by Ron Knight, used under Creative Commons Attribution 2.0 Generic.

Figure 4: Carpal knob in the western crowned pigeon (*Goura cristata*). Modified from Hume & Steel, 2013.

Figure 5: 2 cm carpal knob of the Rodrigues Island solitaire (*Pezophaps solitaria*). Modified from Hume & Steel, 2013.

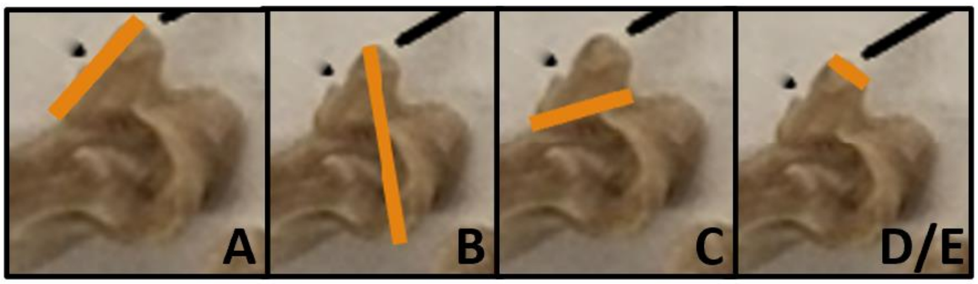

Figure 6: Extensor process linear measurements: A) length from behind the *process alularis* to the distal tip of the extensor process, b) height across the bone from the *facies articularis ulnocarpalis* to the distal tip of the extensor process, c) width of the process base in the dorsoventral plane, d) and right-angle widths of the process tip in the dorsoventral plane and e) the mediolateral plane

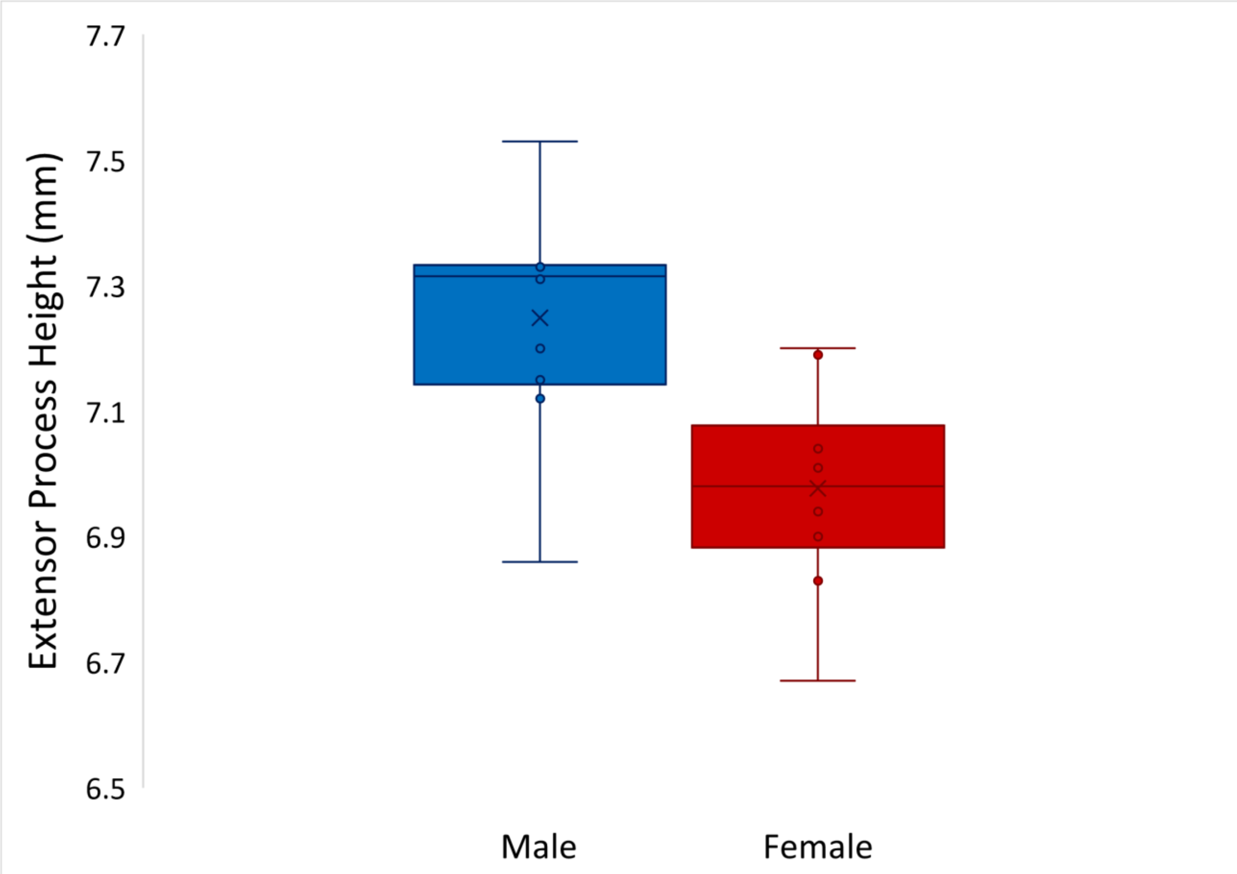

Figure 7: Extensor process height by sex in WWDO. Body size proxy (tarsometatarsus) was not found to be significantly predictive in backwards stepwise regression and is not included here. Whiskers show upper and lower quartile, median is represented by a horizontal line, and mean by an X. Sex significantly predicts extensor process height ($F(1,18) = 3.5877$, $p = 0.002$).

Appendix 2: Full Statistical Results

Table 1: WWDO vs. MODO linear measure statistics: student's t-test of residuals.

Sex	Measurement	Species P value	DF	T-statistic
Male	Carpometacarpus Greatest Length	0.99	17	0.012
Male	Carpometacarpus Major Digit Dorsoventral Width	0.84	17	0.202
Male	Carpometacarpus Major Digit Anterior-Posterior Width	0.59	17	0.546
Male	Carpometacarpus Minor Digit Dorsoventral Width	0.98	17	0.029
Male	Carpometacarpus Minor Digit Anterior-Posterior Width	0.88	17	0.149
Male	Humerus Greatest length	0.80	17	0.259
Male	Humerus Dorsoventral Width	0.94	17	0.072
Male	Humerus Anterior-Posterior Width	0.71	17	0.376
Male	Radius Greatest Length	0.97	17	0.041
Male	Radius Dorsoventral Width	0.92	17	0.103
Male	Radius Anterior Posterior Width	0.98	17	0.027
Male	Ulna Greatest Length	0.94	17	0.074
Male	Ulna Dorsoventral Width	0.84	17	0.205
Male	Ulna Anterior-Posterior Width	0.89	17	0.146
Male	Extensor Process Height	0.96	17	0.047
Male	Extensor Process Length	0.89	17	0.144
Male	Extensor Process Base Width	0.93	17	0.091
Male	Extensor Process Mediolateral Tip Width	0.63	17	0.495
Male	Extensor Process Dorsoventral Tip Width	0.98	17	0.032
Female	Carpometacarpus Greatest Length	0.98	16	0.024
Female	Carpometacarpus Major Digit Dorsoventral Width	0.97	16	0.034
Female	Carpometacarpus Major Digit Anterior-Posterior Width	0.96	16	0.057
Female	Carpometacarpus Minor Digit Dorsoventral Width	0.92	16	0.106
Female	Carpometacarpus Minor Digit Anterior-Posterior Width	0.83	16	0.217
Female	Humerus Greatest length	0.98	16	0.020
Female	Humerus Dorsoventral Width	0.98	16	0.025

Female	Humerus Anterior-Posterior Width	0.93	16	0.090
Female	Radius Greatest Length	0.96	16	0.056
Female	Radius Dorsoventral Width	0.86	16	0.179
Female	Radius Anterior Posterior Width	0.76	16	0.314
Female	Ulna Greatest Length	0.79	16	0.268
Female	Ulna Dorsoventral Width	0.96	16	0.052
Female	Ulna Anterior-Posterior Width	0.87	16	0.171
Female	Extensor Process Height	0.74	16	0.344
Female	Extensor Process Length	0.93	16	0.091
Female	Extensor Process Base Width	0.74	16	0.332
Female	Extensor Process Mediolateral Tip Width	0.85	16	0.187
Female	Extensor Process Dorsoventral Tip Width	0.69	16	0.412

Table 2: WWDO vs. MODO shape statistics: student's t-test of shape ratios.

Sex	Measure	Species p Value	DF	t-statistic
Male	Carpometacarpus Major Digit Shape	0.560	17	0.594
Male	Carpometacarpus Minor Digit Shape	0.947	17	0.067
Male	Humerus Midpoint Shaft Shape	0.308	17	1.051
Male	Radius Midpoint Shaft Shape	0.027	17	2.422
Male	Ulna Midpoint Shaft Shape	0.009	17	2.953
Male	Extensor Process Tip Shape	0.449	17	0.775
Female	Carpometacarpus Major Digit Shape	0.377	17	0.907
Female	Carpometacarpus Minor Digit Shape	0.263	17	1.158
Female	Humerus Midpoint Shaft Shape	0.644	17	0.470
Female	Radius Midpoint Shaft Shape	0.141	17	1.543
Female	Ulna Midpoint Shaft Shape	0.791	17	0.270
Female	Extensor Process Tip Shape	0.274	17	1.130

Table 3: Male vs. Female major bone linear measure statistics: backwards stepwise regression including sex and body size, and univariate regression using sex in cases where body size was not significantly predictive.

Species	Measurement	Sex p Value	Body Size p Value	Model R^2	VIF	Sex p Value Univariate	Univariate R^2
MODO	Carpometacarpus Greatest Length	0.9033	0.0003	0.629	1.21	-	-
MODO	Carpometacarpus Major Digit Dorsoventral Width	0.7099	0.0064	0.425	1.21	-	-
MODO	Carpometacarpus Major Digit Anterior-Posterior Width	0.7965	0.0031	0.473	1.21	-	-
MODO	Carpometacarpus Minor Digit Dorsoventral Width	0.0370	0.3212	0.336	1.21	-	-
MODO	Carpometacarpus Minor Digit Anterior-Posterior Width	0.1040	0.3910	0.206	1.21	0.0417	0.234
MODO	Humerus Greatest length	0.3180	<0.0001	0.725	1.21	-	-
MODO	Humerus Dorsoventral Width	0.5644	0.0199	0.343	1.21	-	-
MODO	Humerus Anterior-Posterior Width	0.4525	0.0792	0.221	1.21	-	-
MODO	Radius Greatest Length	0.4517	0.0014	0.566	1.21	-	-
MODO	Radius Dorsoventral Width	0.3269	0.1421	0.194	1.21	-	-
MODO	Radius Anterior Posterior Width	0.6895	0.0873	0.160	1.21	-	-
MODO	Ulna Greatest Length	0.3924	<0.0001	0.057	1.21	0.1214	0.143
MODO	Ulna Dorsoventral Width	0.7208	0.0117	0.369	1.21	-	-
MODO	Ulna Anterior-Posterior Width	0.1047	0.0258	0.458	1.21	-	-
WWDO	Carpometacarpus Greatest Length	0.0373	0.0034	0.736	2	-	-
WWDO	Carpometacarpus Major Digit Dorsoventral Width	0.5635	0.8069	-0.042	2	0.2809	0.064
WWDO	Carpometacarpus Major Digit Anterior-Posterior Width	0.3687	0.2569	0.226	2	-	-
WWDO	Carpometacarpus Minor Digit Dorsoventral Width	0.0296	0.8945	0.350	2	-	-
WWDO	Carpometacarpus Minor Digit Anterior-Posterior Width	0.7069	0.9655	-0.102	2	0.6152	0.014
WWDO	Humerus Greatest length	0.0458	0.0318	0.631	2	-	-
WWDO	Humerus Dorsoventral Width	0.5349	0.5975	0.018	2	0.1604	0.106
WWDO	Humerus Anterior-Posterior Width	0.2204	0.1149	0.402	2	-	-
WWDO	Radius Greatest Length	0.5577	0.0002	0.722	2	-	-

WWDO	Radius Dorsoventral Width	0.4268	0.7593	0.012	2	0.1504	0.111
WWDO	Radius Anterior Posterior Width	0.4555	0.4090	0.114	2	-	-
WWDO	Ulna Greatest Length	0.4144	0.0002	0.750	2	-	-
WWDO	Ulna Dorsoventral Width	0.7672	0.3043	0.065	2	-	-
WWDO	Ulna Anterior-Posterior Width	0.1075	0.7396	0.111	2	0.0483	0.200

Table 4: Male vs. Female extensor process linear measure statistics: backwards stepwise regression including sex and body size, and univariate regression using sex in cases where body size was not significantly predictive. (Significant p-values are bolded).

Species	Measurement	Sex p Value	Body Size p Value	Model R^2	VIF	Sex p Value Univariate	Univariate R^2
MODO	Extensor Process Height	0.6651	<0.0001	0.666	1.21	-	-
MODO	Extensor Process Length	0.3480	0.0117	0.288	1.21	-	-
MODO	Extensor Process Base Width	0.9162	0.0364	0.229	1.21	-	-
MODO	Extensor Process Mediolateral Tip Width	0.5445	0.7076	-0.075	1.21	0.5149	0.027
MODO	Extensor Process Dorsoventral Tip Width	0.8681	0.2078	0.023	1.21	-	-
WWDO	Extensor Process Height	0.0657	0.4569	0.370	2	**0.0021**	0.417
WWDO	Extensor Process Length	0.3966	0.3609	0.159	2	-	-
WWDO	Extensor Process Base Width	0.6374	0.3651	0.071	2	-	-
WWDO	Extensor Process Mediolateral Tip Width	0.6467	0.9695	-0.086	2	0.4812	0.028
WWDO	Extensor Process Dorsoventral Tip Width	0.2927	0.0383	0.157	2	-	-

Table 5: Male vs. Female shape statistics: student's t-test of shape ratios.

Species	Measure	Sex p Value	DF	t-statistic
MODO	Carpometacarpus Major Digit Shape	0.480	16	0.723
MODO	Carpometacarpus Minor Digit Shape	0.609	16	0.522
MODO	Humerus Midpoint Shaft Shape	0.498	16	0.694
MODO	Radius Midpoint Shaft Shape	0.402	16	0.861
MODO	Ulna Midpoint Shaft Shape	0.018	16	2.635
MODO	Extensor Process Tip Shape	0.870	16	0.166
WWDO	Carpometacarpus Major Digit Shape	0.244	18	1.204
WWDO	Carpometacarpus Minor Digit Shape	0.456	18	0.762
WWDO	Humerus Midpoint Shaft Shape	0.150	18	1.506
WWDO	Radius Midpoint Shaft Shape	0.425	18	0.816
WWDO	Ulna Midpoint Shaft Shape	0.822	18	0.228
WWDO	Extensor Process Tip Shape	0.718	18	0.367

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