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Muscle Mass, Wing Morphology, and Related Flight Mechanics in Passeriforme Birds

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Muscle Mass, Wing Morphology, and Related Flight Mechanics in Passeriforme Birds

A Thesis

Presented to the Department of Biology

College of Liberal Arts and Sciences

and

The Honors Program

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In Partial Fulfillment

of the Requirements for Graduation Honors

Bradley Adam Weinstein

April 27, 2015

Morphological Characteristics in Class Aves Associated with Flight

Flight:

In the time since organisms first came onto land, there has been an evolutionary arms race to fill all the complex niches that exist in terrestrial ecosystems. In order to fill these niches, many animals have become evolutionary specialists, allowing them to conquer new places and roles. There may be no animal specialization more awe-inspiring than that of avian flight. Since their evolutionary divide from a common ancestor shared with reptiles, the body of a bird has changed in many ways in order to be able to leave the ground and conquer the sky.

To understand the evolutionary adaptations of birds, one must think about what is necessary in order to take flight. The main constraint that most animals face with maintained flight is overcoming the force of gravity. Simply put, most animals are just too massive to be able to take flight. The equation for the downward force of gravity (F_g) is:

$$F_g = M \times A_g \qquad \text{(eqn.1)},$$

where M is the mass of the object and A_g is the acceleration due to gravity, which is a constant of -9.8m/s². Thus, the more massive the object, the greater the force of gravity acting upon it.

In order to take flight, the upward force, or lift, produced by an animal must be greater than the downward force of gravity acting upon that animal. In order to create more lift than the amount of gravity acting upon it, there are two possible evolutionary strategies an animal can take: reducing mass or increasing the capacity to produce lift. Birds have made use of both strategies in order to achieve flight. In this paper, I will

discuss these two strategies, as well as several adaptations that are necessary for efficient flight in birds.

Mass reduction:

Class Aves is characterized by pneumatization of the skeleton, which results in a large reduction in overall weight (Hickman *et al.*, 2015). Pneumatization refers to the "honeycomb-like" construction of the bones themselves. The bones are mostly hollow, with struts that span the inner diameter of the bone (Fig. 1). This construction causes a significant decrease in the overall mass of the bird, while not compromising the structural integrity of the skeletal system (Hickman *et al.*, 2015). The skull of the bird is not pneumatized, but features a greatly reduced overall mass and is fused into one piece to increase rigidity. The skull of a pigeon makes up around 0.21% of its overall weight, compared to the 1.25% seen in rats (Hickman *et al.*, 2015).

Along with the reduction in mass of the skeletal system, there is a marked reduction of the mass of the digestive system. Birds make use of their gizzard, a muscular sac used for grinding their food, to speed the digestion process. The gizzard allows the bird to break down food without requiring teeth, an adaptation that greatly reduces the mass of the skull (Louchart and Viriot, 2011). After being ground in the gizzard, the food quickly makes its way through the digestive system. Easily digestible foods, such as berries, can be digested in as little as 30 minutes (Hickman, *et al.* 2015). The stomach morphology of birds is more variable than any other organ in class Aves, due to the high variability in diet of different species of birds (Gill, 2006). The excretory

system of the bird also features a great reduction in mass. There is no urinary bladder and urine is passed out of the cloaca as quickly as it is produced (Gill, 2006).

Feathers are a defining characteristic of birds, and they function in two ways: to decrease overall weight, and to increase lift production. Feathers are extremely lightweight when compared to similar volumes of other bodily tissues (Hickman *et al.*, 2015). More importantly, their mechanical design is extremely useful in lift production. Feathers have a hierarchical design, originating at the quill, which is where the feather attaches to the tissue of the bird. From the quill extends a shaft, known as the rachis. The rachis is strong enough to provide structural support, while still maintaining its lightweight character. Extending from either side of the rachis are barbs, which in turn have barbules extending from them. These barbules have interlocking hooks on either side of them, which lock together, forming a sheet of sorts. Because the barbules can form this sheet, the air is less able to pass through the greatly reduced openings in the feather, thus increasing the effective lift of the bird's wings (Hickman *et al.*, 2015).

Stabilization for flight

Once the bird is in the air, stabilization becomes a major factor in energy conservation; if energy is wasted in muscular contraction for in-air stabilization, it cannot be used for flight. Birds go about this in a variety of ways. Firstly, the non-cervical vertebrae of the bird are fused together, which are then fused with the pelvis (Hickman *et al.*, 2015). These fused skeletal elements provide a rigid framework that can stand up to the stresses produced during avian flight. Also to this end, the rib cage of birds is

braced together with a set of uncicate processes, which essentially act as crossbeams spanning the intercostal spaces (Hickman *et al.*, 2015).

Birds have also evolved muscular adaptations that increase stability during flight. Like a commercial jet, birds keep the majority of their mass below their center of gravity. In order to do this, the major muscles concerned with the force production for flight all originate on the ventral surface of the keeled sternum (Hickman *et al.*, 2015).

Flight Musculature:

Most of the force production powering avian flight is generated by two main breast muscles. These muscles, the *pectoralis major* (PM) and *supracoracoideus* (SC) (Fig. 2), are responsible for the downstroke (power stroke) and the upstroke (recovery stroke), respectively. While both of these muscles originate on the keeled sternum that is characteristic of birds, they attach to their respective levers in different ways. The PM orginates on the keeled sternum, and inserts on the ventral side of the humerus. In contrast, while the SC also originates at the keeled sternum, it attaches to a tendon that loops around the foramen triosseum of the scapulae to attach to the dorsal side of the humerus (Schmitt, 2004; Hickman *et al.*, 2015). Thus, the SC powers the upstroke by using a pulley-like mechanism. While muscle shortening takes place on the ventral side of the bird, the force is directed around the foramen triosseum to the dorsal side of the humerus, thus pulling the wing upwards. This allows the muscle to act in a similar fashion to a muscle on the dorsal side of the body, while keeping the center of mass on the ventral side.

While the PM is the muscle that is mainly responsible for the downward force in the power stroke of the wing cycle, and the SC for the upward force in the recovery stroke, the two often operate simultaneously. Poore, *et al.* (1997) presented a graphic representation of the force production of the SC and PM during the wing cycle (Fig. 3). At the beginning of the downstroke, the PM fires, producing a downforce. The PM stops firing about halfway through the downstroke. The SC begins to fire momentarily before the upstroke begins, helping to slow the downstroke. Since, the PM is causing the humerus to move into a position that stretches the SC past its normal resting length, elastic potential energy is built up (Tobalske and Biewener, 2008). The SC continues to fire after the downstroke ends, producing the upward force for the recovery stroke. The slight overlap of the SC firing while the downstroke is still occurring reduces the lag time between the end of the downstroke and the beginning of the upstroke, making the beat-cycle of the wings more time-efficient (Poore *et al.*, 1997).

Lindström, *et al.* (2000) demonstrated that the thickness of the *pectoralis major* was positively correlated with the overall mass of a bird. These researchers determined that a more massive bird has a predictably thicker PM muscle than less massive birds, which is in agreement with a previous study (Marsh, 1984). This relationship is likely due to the increasing need for lift production for flight as birds get larger. The correlation between PM thickness and body mass is different than what is seen in the SC, which varies much more in regards to proportion of body mass (Marsh, 1984). This is due to the different way in which the SC powers its contraction. As noted above, the SC seems to function not only to power the upstroke, but also to store strain energy, which is the energy that comes from stretching the muscle past its resting length. Tobalske and

Biewener (2008) demonstrated that the SC was a very efficient muscle in regards to its ability to store strain energy and reuse it in returning the wing to its ready position; an estimated 28-60% of the net work of the SC comes from elastic energy storage. This efficiency is important to the flight of the bird as it allows for less energy to be used in returning the wing to its resting position; it also reduces necessary muscle mass. Because less energy is used in recovery strokes, more energy is available during the power stroke for the production of lift.

The correlation between the PM muscle mass and body mass is not likely conserved between all species, however, as differential flight demands may favor larger or smaller flight muscles. In order to avoid obstacles, a bird may need to quickly change its plane of flight. Therefore, a bird that lives in more or less complicated environments would have different muscular demands. For instance, a bird that requires very agile, quick movements may require larger muscles in order to create enough lift to be able to dodge any obstacles it may encounter (eg. predators, tree trunk, etc.). Such flight behavior requires shorter, relatively higher force bursts of muscle contraction. In contrast, a bird that does less agile movements and more sustained, long flights may have relatively lower PM muscle mass, as greater amounts of force are not necessarily required for this particular style of flight.

The muscle fiber profile of the muscle also varies between the PM and the SC. Marsh (1984) determined that the PM shows a greater proportion of fast twitch fibers to slow twitch fibers, as compared to the SC (88%/12% and 58%/42%, respectively). The difference in muscle fiber proportions between the PM and SC is likely due to the differing responsibilities of the two muscle groups. Fast-twitch fibers tend to be

associated with rapid, powerful movements, while slow-twitch fibers tend to be associated with sustained locomotion. The PM is responsible for a powerful downstroke, during which it maximizes the lift created (Hickman *et al.,* 2015). This lift is created by creating a pressure differential between the top and bottom of the wing (Vogel, 2013). Since this differential is maximized when the wing is moving at high velocity, a rapid downstroke would be most effective at producing lift (Vogel, 2013). This relationship is in keeping with to the PM having a greater proportion of fast-twitch than slow-twitch fibers. The SC, on the other hand, has a greater proportion of slow-twitch muscles than fast-twitch (Marsh, 1984). The primary purpose of the SC is to return the wing back to its original position so that the wing cycle can start over. The recovery stroke would be more energetically costly if it was a faster stroke, because more drag would be produced (Vogel, 2013).

The SC does have a moderate amount of fast-twitch fibers (Marsh, 1984), however, as this muscle is responsible for the rapid recovery stroke required for takeoff (Gill, 2006). Because of this mix of fibers, the SC is able to provide the rapid flapping motion necessary for takeoff (Gill, 2006), then allow the strain energy storage mechanism to take over once flight is achieved (Tobalkse and Biewener, 2008). As mentioned previously, a bird that is frequently dodging obstacles would likely require rapid, forceful muscle contractions in order to change flight planes. This functional demand would likely lead to a greater amount of fast-twitch muscle fibers. A bird that has slower, more sustained flight patterns likely has less fast-twitch and more slow-twitch fibers.

The relationship between bird muscle mass and energetically efficient flight creates an interesting impasse; there are two conflicting functional demands associated with flight. Studies show that larger cross-sectional muscles are able to produce a greater quantity of force (Sherwood *et al.*, 2013), which is necessary because flight requires a large amount of power. At the same time, birds need to minimize their weight in order to be able to sustain flight. Many of the traits of birds are thought to be adaptations that minimize weight (Hickman *et al.*, 2015).

These conflicting demands lead to the idea of a dynamic relationship between power production and weight minimization. Due to evolutionary demands, a bird in one evolutionary lineage may maximize muscle mass, while a bird in another evolutionary lineage may have adapted to minimize overall weight. This dynamic relationship of different locomotor demands can be illustrated by thinking of an olympic sprinter and a marathon runner. The ideal sprinter has massive legs muscles, providing huge amounts of force for a short burst of speed. This is comparable to birds that fly low through forests, as they are required to make sudden cuts through the air to avoid vegetation or other obstacles. The marathon runner, on the other end of the spectrum, has very little muscle mass, producing less explosive forces while opting towards longer, sustained locomotion, such as a bird in migratory flight. This analogy is not perfect, however, as many birds exist towards the middle of the spectrum. These birds may quickly create large amounts of lift in one season, then require the endurance to migrate during another season; some birds may encounter both styles in a single day. In these birds, we would expect to see adaptations for both endurance and forceful lift production. Most

birds fall into this category, with a blend of long-term endurance flight patterns with interspersed short-term powerful flight (Gill, 2006).

Wing Morphology and Lift Production:

Morphological differences of the wing itself have also been linked to different styles of flight. Two factors that have a great impact on these differing styles of flight are aspect ratio and wing loading. Both of these variables have been linked to differences in maximum flight speed and lift production (Alerstam *et al.*, 2007; Hickman *et al.*, 2015), and therefore likely differ between birds that occupy different niches in an ecosystem.

Aspect ratio (AR) is a numerical description that can be used to describe a wing's shape (Norberg, 1990). There are multiple formulas for the determination of AR, but the concept is essentially the ratio of length to width of the wing (Hickman *et al.*, 2015). The formula for AR is as follows:

$$AR = L / W \qquad \text{(eqn. 2),}$$

where L is the length from the shoulder socket of the bird to the tip of its longest wing feather, and W is the width of the wing from the leading edge of the wing to the tip of the furthest feather on the trailing edge (Fig. 4). A bird with a long, narrow wing will have a relatively high aspect ratio; conversely, a bird with a short, wide wing will have a relatively low aspect ratio. Evidence suggests that aspect ratio can be used as a predictor for avian flight speed (Gill, 2006; Hickman *et al.*, 2015). Birds with higher aspect ratios (long, narrow wings) tend to fly faster, whereas birds with lower aspect ratios (short, wide wings) tend to fly at a lower velocity (Hickman *et al.*, 2015). This information can be useful in predicting lift production. Fish (1990) demonstrated in flying

fish wings that a wing with lower aspect ratio can create greater amounts of lift at slower flight speeds than wings with higher aspect ratio.

However, the shape of the wing does not solely determine how fast a bird can fly. One must also consider wing loading as a predictive morphological factor of avian flight speed. In order for a bird to achieve flight, the amount of lift produced must exceed the downward pull of gravity due to the weight of the bird. To this end, a heavier bird must fly faster in order to produce enough lift to counteract the downward force (Norberg, 1985). Because of this, heavier birds tend to fly faster than lighter birds (Vogel, 2013). The weight of the bird itself, however, is not an accurate predictor of average flight speed; instead, one must look at wing loading (Alerstam et al., 2007), which is defined by Vogel (2013) as :

$$WL = W / S \qquad\qquad \text{(eqn. 3)},$$

where W is the total weight of the bird and S is the surface area of the wings. From this formula, we can see that a heavier bird with smaller wings will have a higher wing load than a lighter bird with larger wings. Higher wing loads have been associated with greater flight speeds, as the smaller wings need to move faster through the air to generate as much lift as a larger wing produces at slower speeds (Norberg,1985; Alerstam et al., 2007). Wing loading is also associated with decreased maneuverability. Pennycuick (1971) demonstrated that there is a positive correlation between wing loading and the minimum radius of a level banked turn in flight, which was used as a measure of maneuverability; birds with higher wing loading required a larger radius to make the turn. A bird that can make an unbanked turn with a smaller radius

demonstrates greater maneuverability than a bird requiring a greater radius for an unbanked turn.

The combination of these two metrics gives insight into the flight habits of a specific bird or species. As mentioned before, both metrics positively correlate with the speed of the bird in flight, but increasing speed is not always the best flight strategy for a bird. Since faster flight causes objects to approach at greater rates, there is likely an inverse relationship between flight speed and maneuverability. From that information, one prediction could be that a bird that lives and flies through mostly wooded areas would have relatively low numbers for both aspect ratio and wing loading, as the speed of flight is less important than the ability to avoid obstacles. Thus, a forest bird, such as a thrush, would have a lower aspect ratio and wing load than a peregrine falcon, which flies at tremendous speeds.

A final factor that may become a quality predictor of a bird's specific flight habits is the ability to produce lift at a variety of angles of attack. The angle of attack of a bird wing is the angle between the direction of the air current and the plane of the wing. The hypothesis in this regard would be that forest birds would be able to produce more lift at a wider range of angles than birds in a niche that emphasizes speed more. This prediction is because of the increased need for maneuverability in these forest-dwelling birds. A greater range of viable angles for lift production means the bird can effectively avoid obstacles throughout a greater range of aerial positions, which translates to greater maneuverability. Therefore, increased maneuverability is predicted to be associated with lower aspect ratios, decreased wing loading, and increased lift production across a wider range of angle of attack.

Conclusion:

Birds are an interesting field of study for a number of reasons, many of which are related to conflicting evolutionary demands. Birds are required to produce more lift than the downward force of gravity acting upon them. To this end birds have evolved in a number of ways, both in mass reduction and increased lift production. This paper looks into different variables associated with contrasting styles of flight, and how morphological differences allow for these different styles to occur, as well as variables associated with weight minimization.
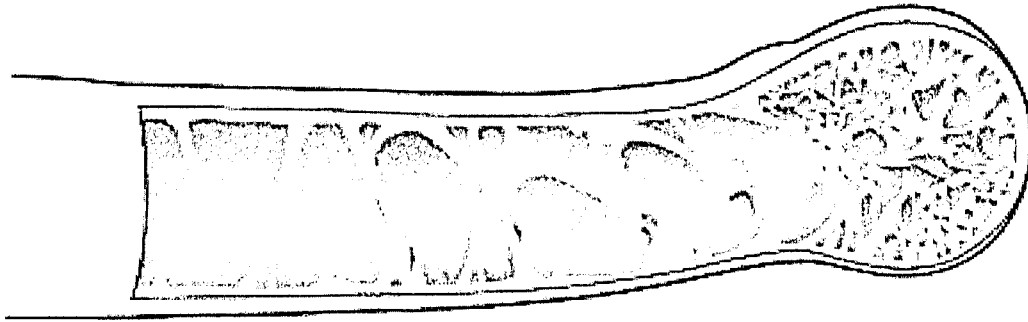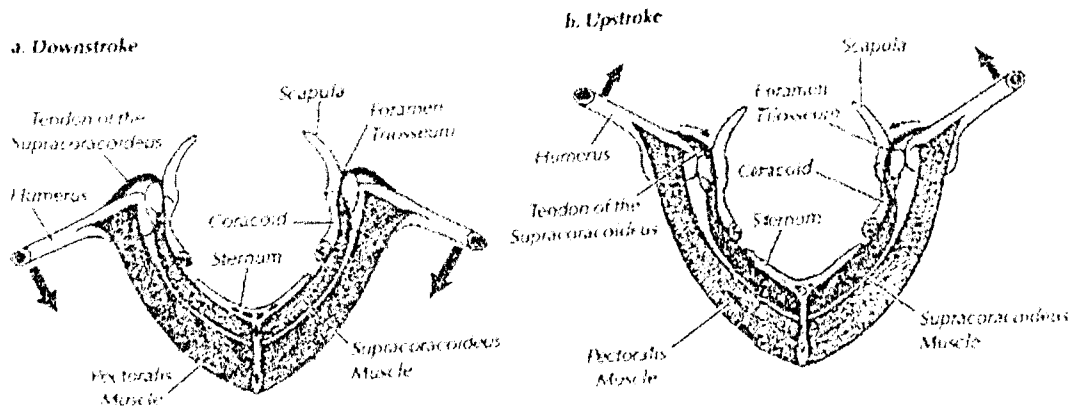
Fig. 1 Longitudinal section of a pneumatized bone. As seen above, the bone is mostly hollow. The struts spanning the inner diameter of the bone increase structural rigidity. Image from Boundless (2014).

a. Downstroke

Tendon of the
Supracoracoideus

Humerus

Scapula

Foramen
Triosseum

Coracoid

Sternum

Supracoracoideus
Muscle

Pectoralis
Muscle

b. Upstroke

Scapula

Foramen
Triosseum

Humerus

Coracoid

Tendon of the
Supracoracoideus

Sternum

Supracoracoideus
Muscle

Pectoralis
Muscle

On the downstroke, the pectoralis pulls tight, pulling the wing bone down.

On the upstroke, the supracoracoideus pulls a tendon that loops around the foramen triosseum; this pulls the wing bone up.

Drawing by N. John Schmitt, from Home Study Course in Bird Biology, 2nd edition, published by the Cornell Lab of Ornithology

Fig. 2 Diagram of Attachment of Flight Muscles. This schematic drawing of the flight muscles found in most birds, drawn by N. John Schmidt of the Cornell Lab of Ornithology) shows the basic arrangement of the muscles. Both flight muscles are attached on the ventral side of the bird which keeps the bird steadier during flight. The *supracoracoideus*, responsible for the upstroke, attaches to a tendon which loops around the foramen triosseum to the dorsal side of the bone, allowing the muscle to pull the wing up.
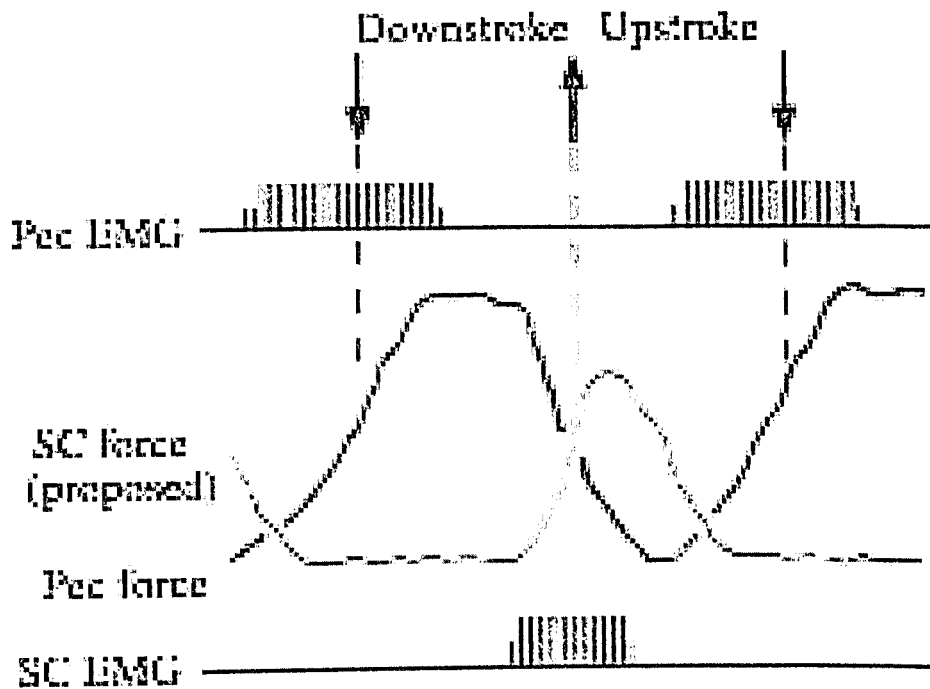
Fig. 3 This figure shows the contraction period of both the SC and PM muscles, represented by the electromyograms (EMGs) on the top and bottom lines of the figure. The EMGs show the time during which the muscle is actively contracting. The relative force produced by each muscle is shown in the middle, represented by the two line graphs. The shaded region in the middle of the graph represents the period during which the contraction of the SC helps to slow the downstroke, then begin the upstroke. In this figure, Pec=PM. (Poore *et al.*, 1997).
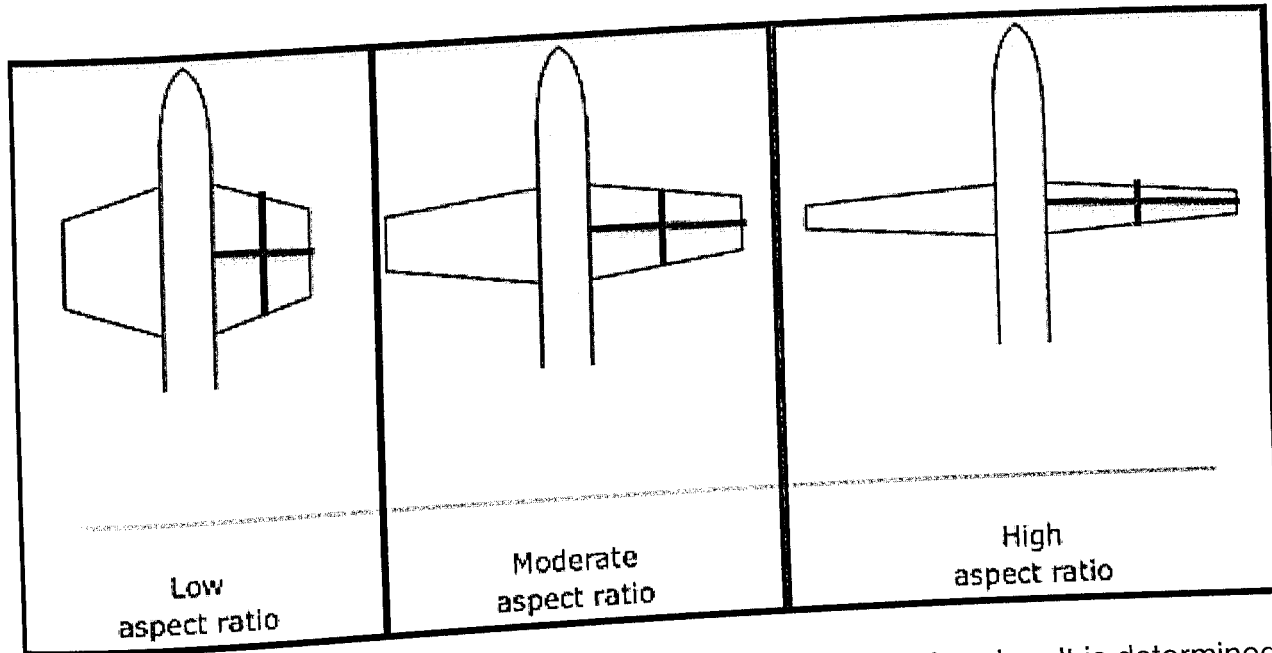
Fig. 4 Aspect ratio is a numerical representation of the shape of a wing. It is determined by dividing the length (horizontal line) of the wing by its width (vertical line), or chord. Image altered from Science Learning Hub- The University of Walkato (NZ) (2007-2015).

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Wing Morphology and Mechanics of Passeriformes Birds

Introduction:

In order to fly, birds (Class Aves) must generate enough lift to offset the downward force of gravity. The two muscles responsible for the majority of lift production in the bird are the *pectoralis major* (PM) and *supracoracoideous* (SC), which are responsible for the power stroke and recovery stroke, respectively. The PM is the larger of the two, as it powers the forceful downstroke of the birds' wings (Tobalkse and Biewener, 2008). The SC, which originates on the sternum, loops around the foramen triosseum to the dorsal side of the humerus (Schmitt, 2004; Gill, 2006; Hickman *et al.*, 2015). This mechanism allows the muscle to efficiently apply force on the dorsal side of the bird, while maintaining the center of weight below the center of gravity for the bird (Hickman *et al.*, 2015). Keeping the majority of weight below the center of gravity is important in maintaining stability during flight, which allows for better energy efficiency. As less muscular energy is used for in-flight stabilization, more can be used for lift production. Muscular thickness of the PM, and therefore mass, has been positively correlated with overall mass of birds (Lindström *et al*, 2000). This relationship is likely due to the increasing demand for lift production with the increasing mass of a bird. This correlation does not hold true for the SC, however, which shows much greater variability in its relative size compared to the bird (Marsh, 1984). This disparity is likely due to the SC being mainly responsible for the return of the wing to its ready position, with minimal responsibility in actual lift production (Gill, 2006).

While the basic morphology of flight musculature within Class Aves is fairly consistent, there is more variation in wing morphology. This differential wing morphology

is associated with niche differentiation. The two main factors connecting wing morphology and flight are aspect ratio and wing loading. Aspect ratio (AR) is a dimensionless numerical descriptor of a wing's shape (Norberg, 1990). There are multiple formulas used to determine AR, but this study will use the method described in Hickman *et al.* (2015), which divides the length of the wing from shoulder to tip by the width of the wing at its widest point. AR has been positively correlated with average avian flight speed (Hickman *et al.* 2015; Gill, 2006), and negatively correlated with lift production capabilities at lower flight speeds (Fish, 1990). A bird with a long slender wing tends to fly at a faster average velocity, which is due partially to their inability to effectively produce lift at lower speeds. Wing loading (WL) is another predictor which has been positively correlated with avian flight speed (Norberg, 1985; Alerstam *et al.* 2007). Wing loading is defined as the weight of the bird divided by the surface area of the wings (Vogel, 2013). Wing loading is not only associated with velocity, but also with maneuverability. Pennycuick (1971) found a negative correlation between wing loading and maneuverability, as birds with greater wing loading required a larger radius to complete a level, banked turn.

The demands of flight may vary dramatically with where and how a bird flies. A bird in open woodlands does not encounter as many obstacles as a bird that flies in the thickest part of a forest. A relatively open environment may require less maneuverability than the complicated forest environment. This study examines the relationship between the different lift producing adaptations and the maneuverability of birds. This study investigates three different hypotheses. First, a bird that lives in the thick of a forest would require greater lift producing capabilities at a greater range of flight angles than

one that lives in an open woodland. This would be due to differential abilities to change planes of flight. A bird that has a greater ability to change planes of flight over a wider range of angles would show more maneuverability in flight. Second, this would suggest that a forest bird has a relatively larger PM. This is due to the fact that thicker muscles have been associated with greater force production (Sherwood *et al.*, 2013), and this greater force production would allow for greater lift production, potentially leading to increased maneuverability. The third hypothesis is that these forest-dwelling birds would have lower aspect ratios and lower wing loading, as both have been associated with increased lift production lift and increased maneuverability. Specifically in this study, I will measure the lift production capabilities of isolated wings at different flight angles, the muscle mass of isolated flight muscles, and morphological differences of isolated wings. I will examine three species of birds, belonging to one of two niches. One species examined is the American robin, which is known to spend much of their time in relatively open woodlands. The other species examined are Swainson's thrushes and wood thrushes, which spend most of their time in the thick of the forest (personal communication, Dr. David Etnier, 2015). All three species belong to the same family, Turdidae, or the true thrushes, which means that there are likely fewer confounding evolutionary variables. These examinations will determine if there are any significant differences in the morphology and lift production capabilities of birds that are known to occupy different niches within an ecosystem.

Methods:

Collection of Specimens:

Birds for this study died due to window strike, or other natural causes, and were collected between the years of 2011 and 2014 under a federal salvage permit issued to Dr. Shelley Etnier (Permit # MB9 8877A-0). The population of this study consists of passeriformes native to Indiana, namely American robins (*Turdus migratorious*) (n=12), Swainson's thrushes (*Catharus ustulatus*) (n=9), and wood thrushes (*Hylocichla mustelina*) (n=6).

Dissection:

The dissection protocol was adapted from Laboratory Anatomy of the Pigeon, 3rd Ed., by Chiasson (1972). Overall body mass of the bird was determined with a digital scale. Feathers were removed from the breast of the bird, then an incision was made to expose the breast musculature from under the skin. The *pectoralis major* (PM) was removed first, as it is located superficially compared to the rest of the breast musculature, and its mass was measured with a digital scale. The *supracoracoideus* (SC) was then isolated to the point where it attaches to the tendon wrapping around the foramen triosseum. The SC was then removed and weighed.

The shoulder joint was found by manipulation of the wing. Right wings were used in all cases unless there was some observed damage to that wing. In those situations, the left wing was used. All remaining musculature and tendon attachments to the joint were bissected, allowing for complete disarticulation of the joint. A pair of surgical scissors was then used to remove the wing, which was pinned to a dissection pan. This

wing was fixed in a position which spread the feathers, but did not allow for any gaps between feathers. This is a position that mimics natural flight position of the wings. The wings dried for a minimum of two days before experimentation.

Wing Morphology:

The isolated wings were photocopied after the drying period was completed, then the image of the wing was cut out. The paper cut out was then weighed. A conversion factor ($138.88 cm^2/g$ of paper) was determined by weighing a piece of comparable paper with a known surface area of $25 cm^2$. The weight of the paper wings was compared to the weight of the conversion paper to determine the planar surface area of the wings (cm^2). The body mass of the bird was then divided by double the planar surface area of the wing, to find the wing loading. The length of the wing was determined by measuring from the shoulder joint to the tip of the furthest feather. The width of the wing was determined by measuring the widest part of the wing at a perpendicular angle to the line of length. Aspect ratio was determined by dividing length by width.

Lift Production:

A lift production apparatus was modified from a lab by Dr. William H. Bernard (Norwich University) (Fig.1). Isolated wings were attached to a ring stand, which was placed on a scale. These wings were then subjected to a headwind produced by a Lasko 20" box fan (mean velocity=16.3 km/h). Wind velocity was measured using a Kestrel wind meter. The wind blew across the wing, perpendicular to the leading edge, creating a lift force perpendicular to the air movement. The scale was able to measure

any lift produced by the isolated wing, as a lower apparent weight on the scale. To account for lift produced by parts other than the wing, the stand was subjected to the wind without a wing attached. Angle of attack was determined by the angle between an imaginary line across the bottom of the wing and the table (Fig.2). Lift production was measured at angles of attack from -30° to 90° relative to the horizon.

Statistical Analysis:

The data were run as a general linear model with species used as a fixed variable to determine if a significant difference was present between species. If a difference was present, a Tukey pairwise comparison was used to determine specific differences between species.

Results:

Muscle Morphology:

Overall mass of the birds differed between species (F=34.98, P< 0.000), with the robin having significantly greater overall mass than the two thrush species, which were similar. The muscular masses of the PM and SC also differed significantly between the birds (F= 65.17, P< 0.000; F=13.71, P< 0.000). Both of the muscles followed the same pattern as the overall mass of the bird. The robin had a significantly greater muscular mass than the thrush species, which were similar.

The ratio of PM mass to overall body mass also differed significantly between the species (F=5.74, P=0.010), with the robin having a significantly higher ratio of PM to body mass than the thrush species. The ratio of SC mass to overall body mass did not

show a significant statistical difference between the two groups. The ratio of SC mass to PM mass also did not differ significantly between the species in this study (F=2.02, P=0.156).

Wing Morphology:

The surface area of the wings differed significantly between species (F=3.47, P=0.048). The robins had a significantly larger surface area than the Swainson's thrushes, while the wood thrushes were statistically similar to both of the other species in the study. The wing loading also differed significantly between the species in this study (F=123.26, P <0.000); the robins had significantly higher wing loading than the thrushes. The aspect ratio of the wings of the species did not differ significantly between species (F=2.53, P=0.102).

Lift Production:

The absolute maximum lift produced differed significantly between the species (F=3.41, P=0.050). The robins produced significantly greater lift than the Swainson's Thrushes, while the wood thrushes were statistically similar to both of the species. The ratio of maximum lift production to overall mass of the birds differed between species (F=34.32, P< 0.000); the thrushes created significantly more lift per gram of body mass than the robins. The angle that created maximum lift did not differ significantly between the species in this study (F=1.72, P=0.202).

Wing Morphology:

The surface area of the wings differed significantly between species ($F=3.47$, $P=0.48$). The robins had a significantly larger surface area than the Swainson's thrushes, while the wood thrushes were statistically similar to both of the other species in the study. The wing loading also differed significantly between the species in this study ($F=123.26$, $P <0.000$); the robins had significantly higher wing loading than the thrushes. The aspect ratio of the wings of the species did not differ significantly between species ($F=2.53$, $P=0.102$).

Discussion:

The robins in this study were significantly larger than either of the thrush species (Table 1). As expected, the mass of both the flight muscles was also larger in the robins than the thrush species. The ratio of PM mass to overall mass of the bird differed significantly between the species, as it was larger in the robins than the thrush species. Thus, the flight muscles of a robin make up a relatively larger portion of the total mass of the bird. This suggests that robins may be able to generate more relative force than the thrushes. This evidence may indicate that the wings of robins are much less efficient than the wings of thrushes at producing lift. As seen in figure 3, robins produce significantly less lift relative to body mass when subjected to the same wind speed, which supports the hypothesis.

Interestingly, the ratio of SC mass to PM mass was fairly conserved between the two groups of birds. There was no significant difference between the two groups,

suggesting similar evolutionary pattern between the two groups in this study. This makes sense, as the American robin and both species of thrush belong to the family Turdidae, otherwise known as the "true thrushes (Gill, 2006)." The relative constancy of the SC/PM ratio suggests that evolutionary pressures to increase force production may operate on the muscles of both the wing upstroke and downstroke.

The results of the wing morphology analysis also support the original hypothesis. There was a significant difference in the wing loading of the birds, as the robins had significantly higher wing loading than the two thrush species. As mentioned earlier, there is a positive correlation between average flight speed and wing loading; heavier birds have to fly faster to create enough lift to stay aloft. Birds that require faster flight speeds to stay aloft are likely less maneuverable, as they would have less time to react to obstacles than slower-flying birds. The aspect ratio of the wings, however, did not differ significantly between the two groups in this study. This once again makes sense, because the birds are closely related in an evolutionary sense. This study did not quantitatively describe any other differences of the wings of these two different groups which may lead to differential lift production, but this may be an interesting area for future research. Some factors to study in the future may be things like wing camber, feather shape, and wing sweep.

The lift production capabilities of these birds support the original hypothesis. The thrush wings produced significantly greater lift per gram of body mass than the robins' wings. This higher lift producing capability suggests that there is an increased ability in the thrushes to change their plane of flight, because the thrushes can produce more upward force per gram of body mass. This ability to change planes can be used to infer

maneuverability. Since the thrushes have greater relative lift producing capabilities, they can change planes faster, and are thus more maneuverable.

The thrush wings also seemed to be able to produce lift over a wider range of angles of attack. There was no significant difference between the angle at which maximum lift was produced between the two groups, but the decline in lift production after maximum lift was more shallow in the thrushes than the robins (Figure 3); more angles produced a relatively high amount of lift from the thrush wings than the robin wings. This wider range of lift production suggests greater maneuverability in the thrushes than the robins. Since the thrushes can produce lift over a wider range of angles, they can change their plane of flight in a greater variety of flight situations, suggesting greater maneuverability.

Overall, the evidence provided in this study suggest that morphological changes associated with differing microniches in an ecosystem may be responsible for increased maneuverability in flight. The birds that live in the thickest part of the forest, the thrush species, exhibited lower wing loading and were more efficient at producing lift over a wider range of angles. While the study supports the hypothesis that there may be some morphological differences in the wings that creates this differential lift production, the research was unsuccessful in determining exactly how this happens. Future studies in this field may look into more intricate morphological factors of these wings in hopes of determining which factors are most important to the lift-producing capabilities of the wings.
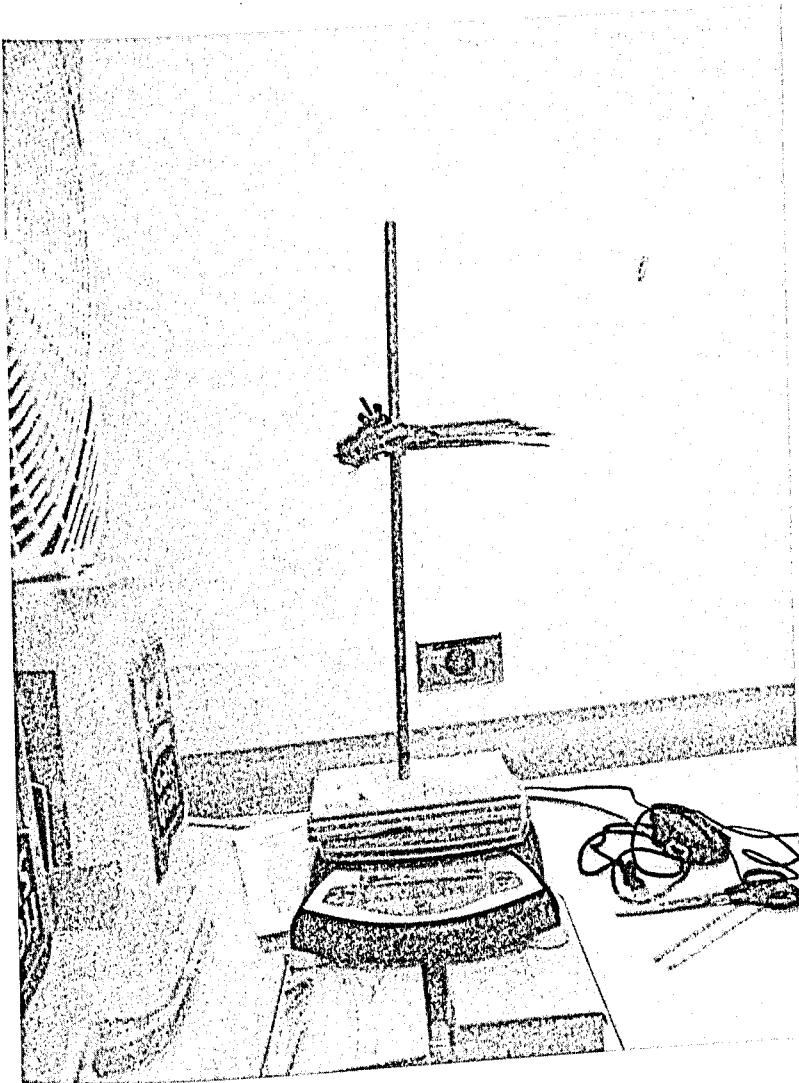
Fig. 1 Lift apparatus, modified from a lab written by Dr. William H. Bernard. The air from the fan flows over the wing, producing a lift force. This lift is measured by the scale.
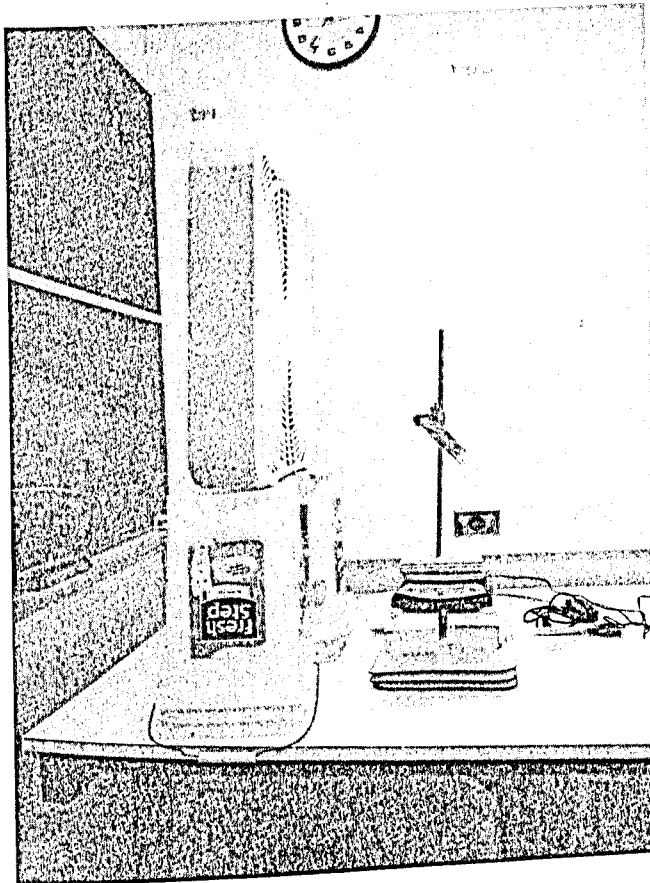
Fig. 2 Angle of Attack, this wing is shown at a 45° angle of attack. The angle of attack is measured as the angle between the horizon and a flat line along the bottom of the wing.
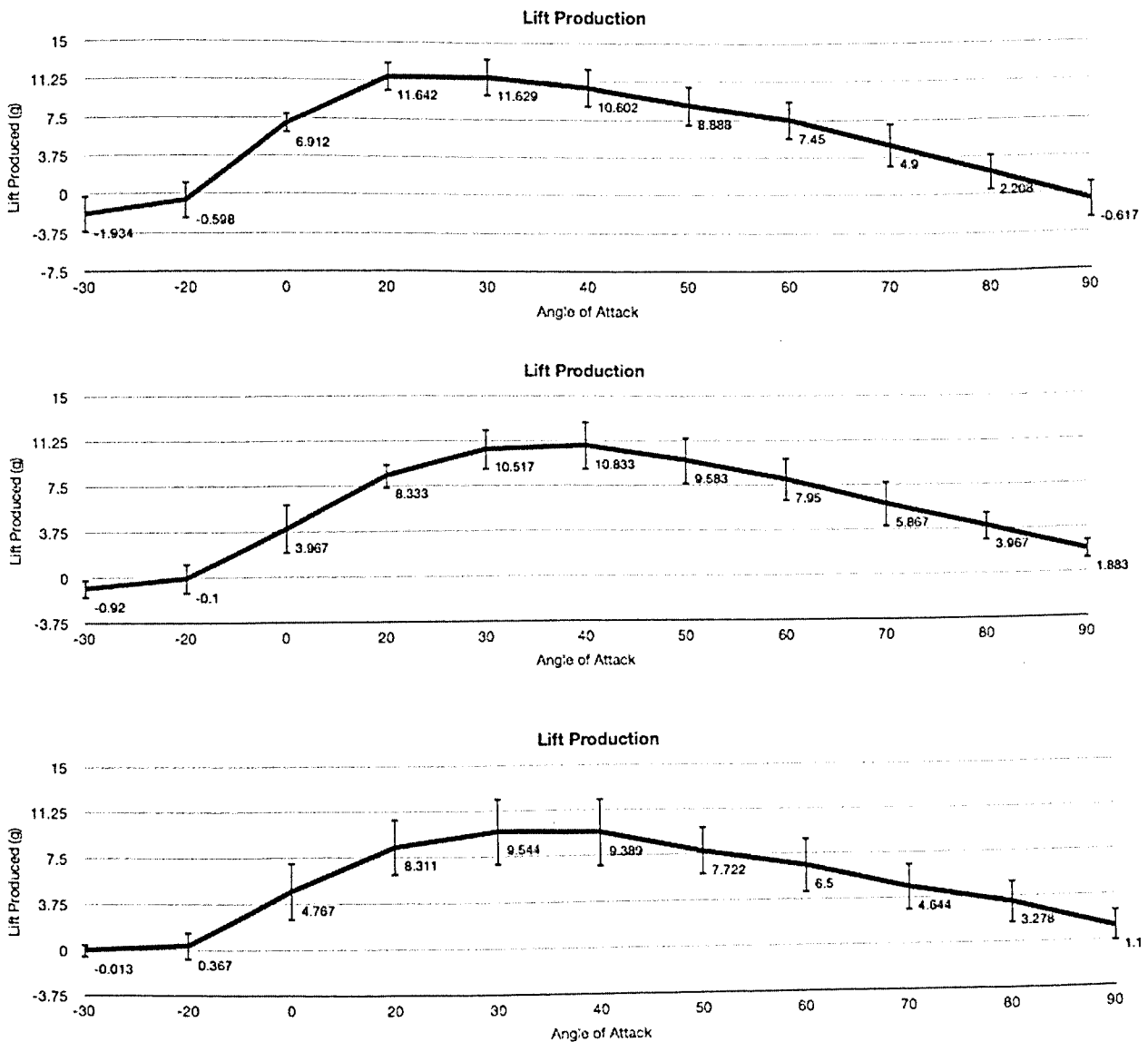
Fig. 3 Lift production capabilities of studied species varies over angle of attack. The lift production capabilities of the three species investigated are summarized in this figure. The mean lift production at each angle is shown. The error bars indicate standard error. The American robin (top) had a peak at 20°, the wood thrushes (middle) had a peak lift production at 40°, and the Swainson's thrushes (bottom) had a peak lift production at 30°.

	American Robin	Swainson's Thrush	Wood Thrush
% PM	9.279 (1.952)	7.57 (0.927)	7.14 (0.652)
% SC	0.801 (0.166)	0.661 (0.246)	0.845 (0.231)
SC/PM	0.0899 (0.0262)	0.0888 (0.0352)	0.1179 (0.0291)
Body Mass	73.816 (10.398)	32.644 (14.335)	38.600 (8.529)
SA	167.39 (22.22)	106.66 (30.3)	99.068 (9.568)
AR	1.71 (0.0717)	1.849 (0.235)	1.86 (0.145)
WL	0.4363 (0.0577)	0.30011 (0.0424)	0.3889 (0.0721)

Table 1. Table summarizing morphological measures investigated in the study. The means of the different variables are shown in this table, with the standard deviation in parentheses. The muscular variables studied were the percentage of body mass resulting from the *pectoralis major* (% PM) and the *supracoracoideous* (% SC), as well as the ratio of the *supracoracoideous* mass to the *pectoralis major* mass (SC/PM). The morphological variables measured in this studied were the surface area of both wings (SA), the aspect ratio of the isolated wing (AR), and the wing loading (WL) calculated by body mass divided by surface area.

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