

Chapter 12

Navigating Functional Landscapes: A Bird's Eye View of the Evolution of Avialan Flight

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ABSTRACT

One of the major challenges in attempting to parse the ecological setting for the origin of flight in Pennaraptora is determining the minimal fluid and solid biomechanical limits of gliding and powered flight present in extant forms and how these minima can be inferred from the fossil record. This is most evident when we consider the fact that the flight apparatus in extant birds is a highly integrated system with redundancies and safety factors to permit robust performance even if one or more components of their flight system are outside their optimal range. These subsystem outliers may be due to other adaptive roles, ontogenetic trajectories, or injuries that are accommodated by a robust flight system. This means that many metrics commonly used to evaluate flight ability in extant birds are likely not going to be precise in delineating flight style, ability, and usage when applied to transitional taxa. Here we build upon existing work to create a functional landscape for flight behavior based on extant observations. The functional landscape is like an evolutionary adaptive landscape in predicting where estimated biomechanically relevant values produce functional repertoires on the landscape. The landscape provides a quantitative evaluation of biomechanical optima, thus facilitating the testing of hypotheses for the origins of complex biomechanical functions. Here we develop this model to explore the functional capabilities of the earliest known avialans and their sister taxa. This mapping allows us to determine where they are placed on the landscape and how phylogenetic trends may course over the landscape. Moreover, the mapping develops a novel tool for assessing potential selection pressures and directions using the quantitative tools developed for adaptive landscapes. Combining these findings with previous work on the ontogeny of the flight stroke, especially in chukar partridges, allows us to test whether this widely used proxy is really suitable and whether we can use ontogenetic trajectories for reconstructing the evolutionary trajectory of the nonavialan theropod to bird transition.

INTRODUCTION

What does it take to fly? This simple question pervades all aspects of research into the origin of birds. For decades it was assumed that feathers were the key innovation that determined flight capability, and their presence was the direct

result of an adaptation for aerial locomotion (Heilmann, 1926; Regal, 1975; Feduccia, 1996; Czerkas and Feduccia, 2014). The recent feathered dinosaur renaissance, led by findings from the Middle-Late Jurassic and Early Cretaceous of China has not only put an end to that line of reasoning, but also increased our knowledge of

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early-diverging avialans many times over (O'Connor and Zhou, 2015), solidified the link between nonavian theropod dinosaurs and birds (Makovicky and Zanno, 2011; Brusatte et al., 2014, 2015; Xu et al., 2014), and provided us with a trove of feathered sister lineages both predating and postdating the earliest birds (Xu et al., 2003, 2011, 2014, 2015; Zhang et al., 2008; Hu et al., 2009, 2018; Han et al., 2014).

Prior to these discoveries the phylogenetic, temporal, and morphological gap between *Archaeopteryx*, the first bird, and its closest relatives was significant, making reconstructions of potential evolutionary pathways through the transition controversial and speculative (Nopsca, 1907; Heilmann, 1926; Ostrom, 1974; Martin, 1983; Norberg, 1985; Feduccia, 1996; Dudley et al., 2007). New information, including details from the use of laser-stimulated fluorescence, or LSF (Falk et al., 2016; Kaye et al., 2015; Kaye et al., 2019a, 2019b; Wang et al., 2017; see also Serrano et al., chapter 13), and a better understanding of how skeletal, integumentary, and other soft tissues evolved across this transition are influencing biomechanical reconstructions of early flight potential and behavior. As that new information is combined with modeling work (Burgers and Chiappe, 1999; Han et al., 2014; Dececchi et al., 2016; Serrano and Chiappe, 2017; Serrano et al., 2018; see also chapter 13) and investigations of modern nonflight-related wing functions (Tobalske and Dial, 2007; Jackson et al., 2009; Fowler et al., 2011; Heers et al., 2014, 2016), we begin to understand not only what features flying organisms possess, but also what minimum values are necessary for these features to permit flight, even if it is weak and of short duration. Here we set up a novel framework for addressing how to evaluate the biomechanical gap between fliers and their antecedents.

Landscapes have played a central role in interpreting evolutionary change. Wright (1932) introduced the adaptive landscape as a tool for use with population genetics and fitness. Simpson (1944, 1953) modified it for discussions of how phenotypic variation can be mapped to fit-

ness. Simpson also expanded this concept from its origin in population genetics to large-scale adaptive evolution across species. In their current usage, adaptive landscapes describe the relationship between mean population fitness and mean population trait values across a pool of populations (Lande, 1976, 1979; Schluter, 2000; Arnold et al., 2001) where traits are typically phenotypic in nature. The phenotypes measured between populations are required to be equivalent, thus necessitating the population samples to be either of the same or closely related species. However, because population fitness is dependent upon external factors, such as local climate and ecology, as well as internal factors, such as genetic drift, the landscape can not be static and is instead more appropriately considered a continually shifting "seascape" (Mustonen and Lasig, 2009; Steinberg and O'Stermeier, 2016). These properties make the use of adaptive landscapes difficult over long periods of time.

However, the approach of developing landscapes to interpret multidimensional data has merit. Strictly, though, adaptive landscapes may be impossible to apply to evolutionary events in deep time, simply because of the length of time involved. The fitness of populations of extinct species cannot be determined beyond their presence or absence (survival or extinction), producing a rather rarified, binary z-axis. However, adaptive landscapes offer quantitative properties that can be used to calculate a variety of variables relevant to evolutionary biology, including modeling drift, adaptation, evolutionary rates, and developmental processes underlying adaptive evolution (Rice, 2004; 2012).

We propose a novel landscape approach to examine evolutionary variation. Instead of a landscape determined by fitness or survival, we propose one calibrated on physical limitations. The axes are defined by phenotypic measures that are as orthogonal to one another as conceptually possible to maintain some semblance of independence. In combination, these axes create a space wherein functional inferences can be mapped. We call this landscape a functional

landscape. Although this landscape does not directly test function, it maps where the observed, or estimated, phenotypes of taxa lie and presents a manifold by which we can draw conclusions about how particular functions map across those taxa.

To introduce this functional landscape, we present an example using powered flight and the origin of birds. Powered flight requires an aerofoil of sufficient surface area and sufficient thrust integrated over mass. Higher thrust generation at a given mass reduces the required aerofoil surface area. However, in animal-powered flight, the aerofoil itself is used to produce thrust and, in most cases, lift. Therefore, increasing aerofoil area is constrained by the requirement of increased flight muscle power. In general, increased muscle power requires increased muscle mass, which increases body mass, thereby requiring a larger aerofoil. These constraints put severe limitations on extreme biomechanical functions like powered flight, especially when considering that all other physiological functions of the animal are present as well.

Starting with first principles, we limit our functional landscape to three basic factors: body mass, wing area, and pectoral muscle mass. These essentially capture the fundamental aspects of flight: the mass to get airborne, the lifting surface size, and the power to drive the aerofoil. To limit autocorrelation, we subtract pectoral muscle mass from total body mass. These three factors are used only for the discussion of the potential of powered flight. Performance estimates and flight initiation, maneuverability, speed, efficiency, and landing cannot be deduced from these factors and require further information on wing aspect ratio, feather variation, body shape, muscle physiology, and tail shape, to name a few. However, our intent is that our simple functional landscape will result in a quantitative manifold so we can compare where different functional repertoires exist, trace evolutionary hypotheses, and plot potential routes through the landscape as hypotheses of evolutionary change.

METHODS

To obtain the largest and most diverse sample in terms of taxonomy, behavior, ecology, and morphology of extant flying birds we used published data that directly measured specimens (Heers and Dial, 2015; Wang et al., 2018). We also included measurements from metaanalyses (Greenewalt, 1975; Alerstam et al., 2007; Serrano et al., 2017; Wang et al., 2018). No flightless extant birds were used in this introductory analysis. Body masses for fossils were estimated from a combination of femoral length (Christiansen and Farina, 2004), femoral circumference (Campioni et al., 2014), and 3-D reconstructions (Chatterjee and Templin, 2007; Dyke et al., 2013) to give a range of values, instead of a single value, because of the importance associated with this metric. For nonavian theropods, primary feather length, when present, was either taken from the literature or was measured directly from images. In the latter case we verified our technique against other elements with recorded values in the literature; in all cases they differed by no more than 2%. For early-diverging birds we chose to use the dataset of Wang et al. (2018) with the addition of femoral lengths taken from several sources: Mayr et al. (2007) for *Archaeopteryx*, Chiappe et al. (2008) for *Confuciusornis*, and Benson and Choiniere (2013) supplying the rest. We chose to take our forelimb metrics from a single source to maintain a consistent measurement pattern for these taxa. Wing areas of extant birds are from Greenewalt (1975). Wing areas for fossils were estimated by following the methodology outlined in Dececchi et al. (2016) or taken directly from Wang et al. (2018) based on the multidimensional approach suggested by Serrano et al. (2017).

Pectoral muscle mass data of extant birds was taken from Greenewalt (1975). Only masses for the pectoralis major were used, in order to limit our landscape to the downstroke, which represents the most rudimentary requirement for flight. The pectoralis complex represents the majority of the flight muscle mass in extant birds, comprising 60% or more of the total fore-

limb mass in many birds (Hartman, 1961; Biewener, 2011). Other forelimb muscles are important for dynamic aspects of flight such as takeoff and landing (Dial, 1993). However, the pectoral muscle is the primary downstroke muscle. One major issue in comparing extant birds with earlier-diverging birds, and especially early-diverging paravian theropods, is the change of the supracoracoideus' role in the flight stroke. Due to the absence of a triosseal canal in nonavian theropods and the earliest-diverging avialan taxa, the supracoracoideus could not act as a wing elevator. Nor was there a ligament-based stabilization system for the shoulder joint, but instead a muscle-based one in nonavian taxa. A ligamentous system did not evolve until well after the transition from nonavian theropod to bird (Baier et al., 2007). In a muscle-based system, the shoulder and back muscles were likely used to elevate the wing as well as stabilize the glenoid (Baier et al., 2007). The forelimb muscles likely had a larger role in wing action, similar to what is seen in nonsteady aspects of modern bird flight (Dial, 1993). To minimize the effect of such a drastic change in the muscle proportion, as a percentage of both the flight muscle and the total body, and the shifting role of the pectoralis minor back/shoulder musculature along this transition we chose to focus only on the mass of pectoralis major as its role as the major wing depressor and its thrust generator should remain constant.

Pectoral muscle masses were estimated for all fossil taxa. Extant birds range from 6% in the Red-throated loon to 30% in the Stripe-tailed hummingbird. A value of 10% was used to estimate pectoral masses for Mesozoic birds and nonavian paravians. This figure was chosen as it: (1) represents the lower bounds seen in competent extant flying birds (Greenewalt, 1975) and bats (Bullen and McKenzie, 2004) and (2) corresponds to the flight muscle mass estimates generated using 3-D volumetric models of the paravians *Microraptor* (Allen et al., 2013) and *Archaeopteryx* (Allen et al., 2013; Heers et al., 2016). These may be higher than what was pres-

ent, given the absence of sternal keels in these taxa. Sternal keels are also absent in early-diverging birds such as *Sapeornis* and *Jeholornis* (O'Connor et al., 2015; Zhao et al., 2017) and highly reduced to absent in all but the most mature specimens of *Confuciusornis* (O'Connor et al., 2015) further implying relatively rudimentary flight capabilities of these taxa. The lower bound for extant birds is in flightless ratites. The pectoral muscles in the ostrich comprise less than 2.4% of their body mass (Dijana et al., 2010), giving a lower bound for paravians. Extant flightless neognath birds have pectoral mass percentages between 8%–15%, but using them as flightless proxies is likely confounded by their relatively recent evolution to flightlessness (McNab, 1994). In addition, relative forewing length (skeleton forelimb to hindlimb) is between 39%–45% in ostriches (Gatesy and Middleton, 1997; Middleton and Gatesy, 2000), whereas it is 68%–76% in *Microraptor* (see Dececchi et al., chapter 11) and the ability to generate aerodynamic forces (Davis, 2005) is significantly smaller in the ostrich than in these paravians, suggesting again that they possessed larger pectoral limb muscles. The pectoral muscles of extant crocodylians make up only 0.7% of their body mass (calculated from data from Allen et al., 2013), though they also have proportionally smaller pectoral limb masses than paravians, but more similar to earlier-diverging theropods (Allen et al., 2013). Therefore, for nonparavian theropods we used an estimate of 2% for pectoral masses with the exception of 1% for short-armed tyrannosaurids.

All supplemental data used is hosted at Open Science Framework (https://osf.io/26ka8/?view_only=74c334b283704479b7682871772cbb35).

RESULTS

Beginning with two variables, body mass to pectoral mass and body mass to wing area yield correlated and well distributed plots (fig. 1). In extant birds, wing area is well predicted by mass ($r^2 = 0.91$) and pectoral mass by body mass ($r^2 =$

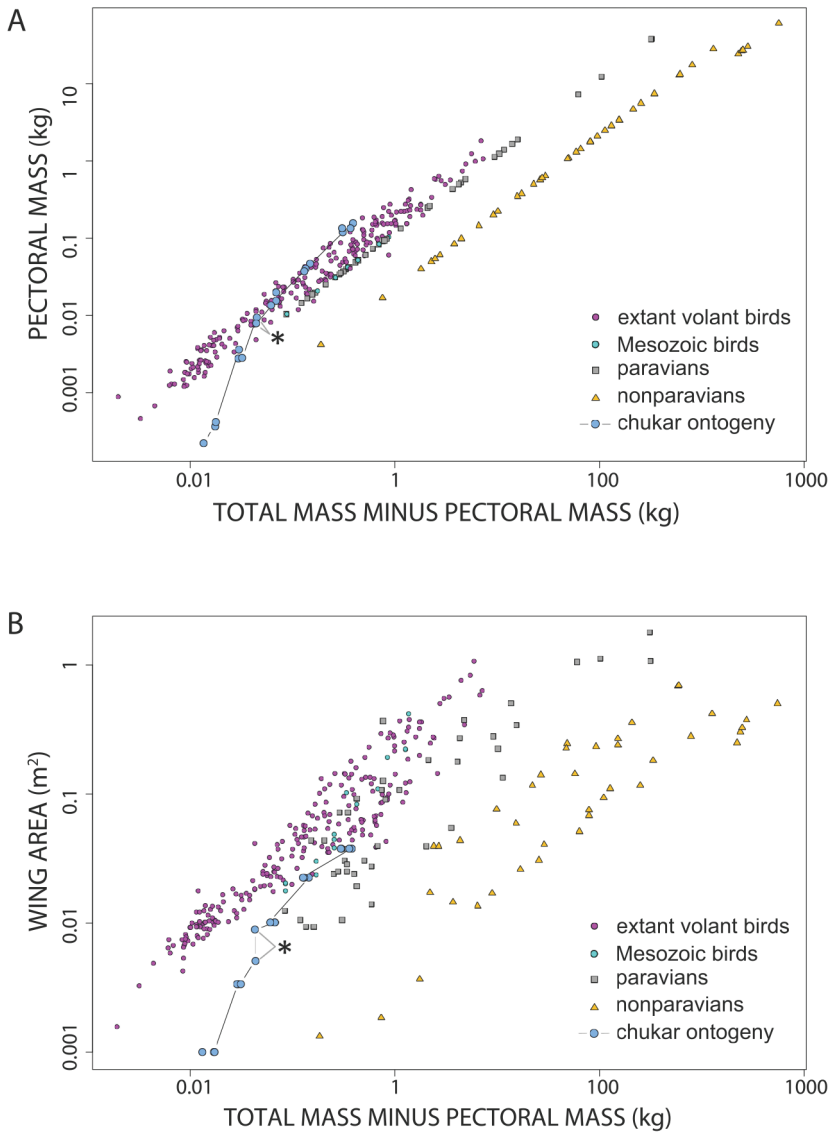


FIG 1. Log axis scatterplots of body mass, pectoral muscle mass, and wing area for extant and Mesozoic birds and nonavian theropods. The asterisk indicates the range where chukar chicks fledge.

0.97). Pectoral mass plots linearly for the fossil taxa because of the simple estimates used. However, even with the generous 2% of body mass estimated for pectoral muscle mass for nonparavian theropods, they plot at a lower intercept than values for extant birds. The 10% pectoral estimate used for paravians and fossil birds aligns them to the lower boundary of extant birds (fig.

1A). However, wing area is more directly estimated from fossils and these taxa plot at well below the lower bounds of extant birds (fig. 1B). The one exception is *Microraptor* (IVPP V13352), with its lower mass estimate of 0.88 kg and wing area of 0.1051281 m².

Chukar values were used from Heers et al. (2015). These individuals represent an ontoge-

netic range from 3 days posthatching (dph) to 100 dph. In both graphs, chukar ontogeny plots on a relatively directed path into the range of extant birds.

When combining these three factors to construct a landscape, the data creates a surprisingly well-resolved surface (fig. 2). The spline is plotted as a smoothed regression through the entire dataset and no taxon deviates greatly from this spline. Extant birds lie along a distinct ridge on the manifold, with Mesozoic birds, paravians, and nonparavian theropods falling further downslope, respectively. As in the 2-D plots, chukar ontogeny traces a trajectory from nonparavian theropods to extant birds and lies close to the regression surface.

DISCUSSION

Unsurprisingly, the relative phylogenetic proximity of different theropod groups to birds is reflected in their mass to pectoral mass to wing areas. This relationship describes a complex manifold with extant birds occupying a sharp ridge with their antecedents, generally, at lower elevations. The lower elevations for these antecedents would be even steeper if more conservative estimates for pectoral masses were used. The ridge extant birds occupy is shaped into a ridge because of a few birds with relatively high wing areas but low pectoral masses. The sharp boundaries of where extant birds plot on the landscape implies birds may be operating within high levels of constraint to the variables of body mass, wing area, and pectoral mass. Variation in any variable has functional consequences on the other variables that in turn affect powered flight. Birds appear to be functioning in a very constricted range of these variables to maintain powered flight.

Mesozoic birds and many nonavian paravians plot within and just downslope of extant birds. The surface extending from them to nonparavian theropods forms a smooth surface, suggesting the variables are mapping a continuum between species. By this, we mean that the vari-

ables observed in these taxa do not seem to obviously deviate from a simple landscape.

If we consider this functional landscape as a surface where evolutionary change must traverse, we can ask how particular starting points may track to end points. The shortest traverse from nonavian to avian realms is at small body size. In this region, nonvolant and volant taxa approach each other, implying that functionally, the step to flight may be easiest at small body sizes. This correlation has been suggested by many others, but the landscape provides a visual representation of the potential route. Larger-bodied nonparavian theropods not only have to climb further along the landscape to approach the avian realm, but also have to climb a steeper slope. Slope and distance are used in adaptive landscape modeling to estimate evolutionary trajectories (Rice, 2004). One could use this functional landscape to estimate the evolutionary “effort” required for a large-bodied nonparavian to either track directly upslope, track along a contour, or reduce body size and then track upslope or along contours.

Very small body size evolved in the bizarre Scansoriopterygidae. This radiation of maniraptorans evolved membrane-based wings supported by elongate fingers. Adult specimens of *Yi qi* and *Ambopteryx longibrachium* have been estimated to have body masses of approximately 300 g, making them some of the smallest nonavian theropods (Xu et al., 2015; Wang et al., 2019). This radical departure from the theropod body plan and novel wings may have been facilitated by their very small body size, making them more capable of crossing into new locomotory realms. Their ability to move with powered flight is questionable, but their foray into at least a gliding mode seems reasonable given their small body size.

An argument using an ontogenetic example of the origins of bird flight comes from juvenile chuckars. Young individuals not yet capable of flight can use their wings to assist in incline running (Dial, 2003). Interestingly, the youngest chuckar samples (3–8 dph) plot in the ranges

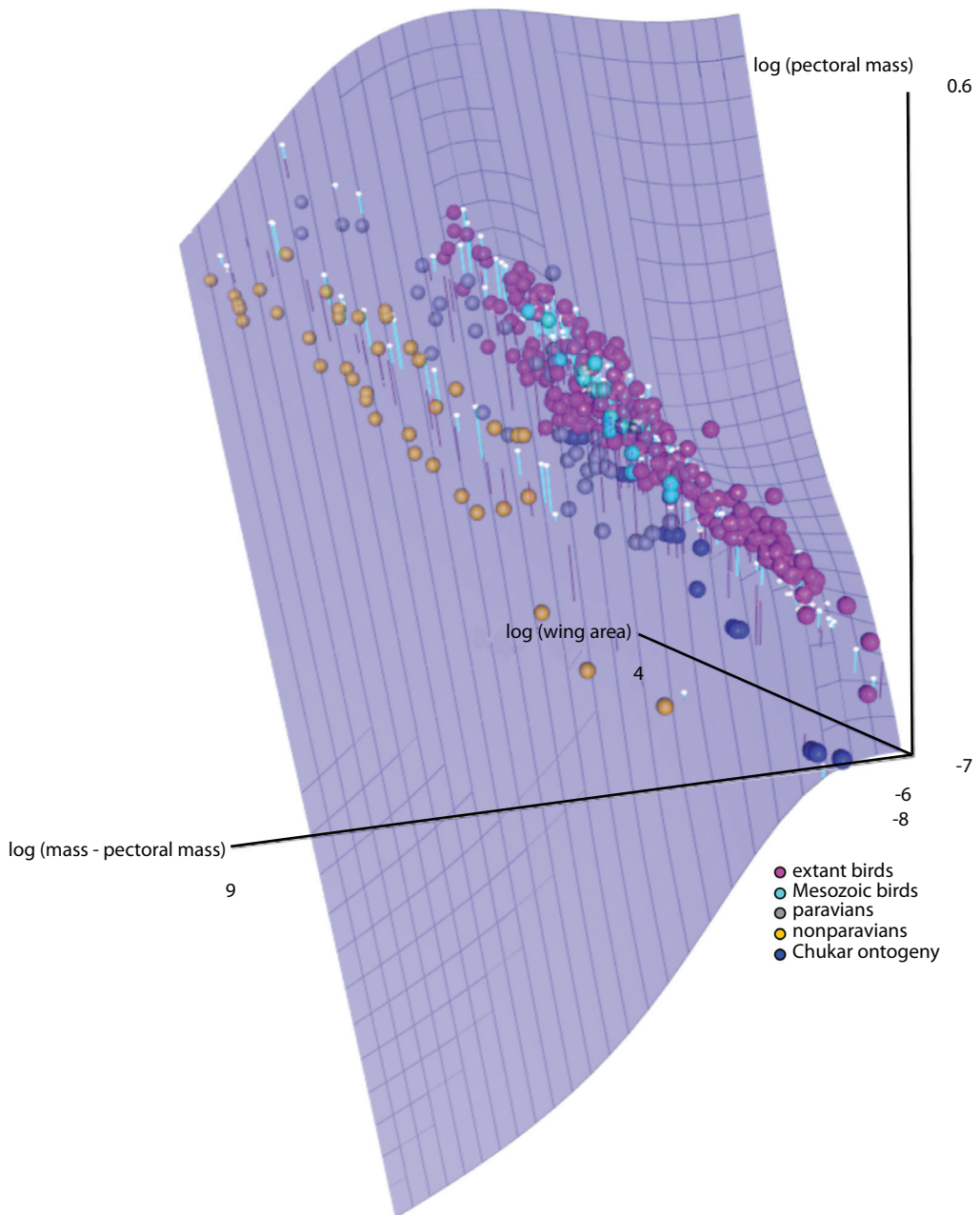


FIG. 2. Three axes scatterplot of a functional landscape of Theropoda flight capability as estimated by logged body mass, pectoral muscle mass, and wing area. The surface is a smoothed regression through all the points. The surface has a discrete ridge on which extant volant birds lie on whereas all nonavialan theropods plot on its slope.

from nonparavian theropods to paravians. Chukars of 0–5 dph are capable only of low-angle wing-assisted incline running. At this age, these birds are less than 20 g in body mass and either crawl or asymmetrically flap their wings to produce forces of approximately 6%–10% of their body weight (Jackson et al., 2009; Heers et al., 2011, 2014). They are able to ascend inclines of less than 65°, slightly greater than the level that they can ascend using their legs alone (55°–60°) (Bundle and Dial, 2003; Dial et al., 2006). However, any growth trajectory would be expected to pass this route given that birds are not born in their adult form. Chukars fledge between 14 and 18 dph, and this is the range where the chukar trajectory passes into the realm of extant birds. In spite of this extreme ontogenetic trajectory, chukar ontogeny still plots relatively close to the functional landscape.

Further refinements are required before evolutionary models across this functional landscape can be made. In particular, more accurate estimates of body mass and pectoral mass are needed to better shape the landscape. Directly preserved body outlines would be particularly helpful in this regard with a range of obscured and otherwise invisible ones already revealed by LSF imaging (Falk et al., 2016; Wang et al., 2017; see also Serrano et al., chapter 13). Other variables, such as flapping rate, metabolic costs, wing aspect ratio, and patagium and feather properties may prove useful to differentiate between alternative hypothetical evolutionary routes. Additionally, anatomical variables, such as bone segment lengths would help construct biomechanical models at each position on the functional landscape. Furthermore, as the interrelationships among the nonavian paravian groups and early diverging birds get more clearly resolved (see discussion of said topic in Pittman et al., chapter 2), accounting for phylogenetic signal among these variables, as well as discussions on clade-specific apomorphies that could alter flight style and ability, can and must be incorporated. Currently there is little evidence for significant differences in the material proper-

ties of the wings, distribution of muscle fiber types or metabolic rates among paravian lineages, but if discovered they could lead to an expansion or contraction of the landscape volume occupied by that group.

Although there are many caveats to estimating body mass, the major cause of concern here is our estimation of the proportion of fossil taxal pectoral muscle masses. There have been previous estimates of exceedingly low values (0.5% of body mass for *Archaeopteryx* according to Bock, 2013) that resemble those seen in flightless raptorial birds such as the kiwi (McNab, 1994) and would, if verified, preclude any aerial locomotion in this taxa. We reject this extremely low mass estimate for flight muscle reconstruction for several reasons: (1) Recent 3-D volumetric approaches estimate the pectoral limb mass at greater than 12% total mass (Allen et al., 2013). This mass estimate does include the wing skeleton (though not feathers), but as skeletal mass averages only around 6% of total mass in extant birds (Martin-Silverstone et al., 2015) it is unlikely this is a major factor. It is also unclear if this estimate includes all the flight related musculature in the trunk region especially shoulder and back muscle, which would have a greater role in the flight stroke and wing stabilization before the origin of the ligament-based wing system of extant birds. (2) Although flight muscles in extant birds often account for a significant percentage we do know that juvenile birds often fledge with a significantly lower volume of flight muscles than adults. In chukars fledging occurs with flight muscles between one-half and two-thirds the adult percentage, with similar values for sparrows and wrens, with pectoral muscle mass making up around 10% of total body mass (Austin and Ricklefs, 1977; Heers and Dial, 2015; Heers et al., 2018). This supports recent work suggesting that it is likely wing size rather than muscle size that is a major limiting factor on the origins of flight (Heers et al., 2018). There is also evidence that suggests wing bone growth rate is the strongest influence on fledging time, suggesting that for longer-winged birds getting the wing

size, not the pectoral size, right is what controls when they first take to the air (Carrier and Auriemma, 1992). For these reasons we feel that, at least for large-winged paravians near the transition, flight muscle size should not be considered an a priori reason to exclude them from the avialan realm on the functional landscape, and that it should be examined along with other variables like wing size (as estimated by wing loading) and shape when estimating flight potential, ability, and style. As an example, although *Archaeopteryx* was relatively light, at approximately 300 g for the largest specimens (Elzanowski, 2002), and surely had relatively small pectoral muscles originating on its unkeeled sternum, this taxon may still compare well with extant volant birds in terms of ability to achieve the thresholds of powered flight. Pigeons have similar body masses (300–400 g) but have pectoral muscle masses of up to 20% their total body mass. The wing areas of both taxa are similar (Dececchi et al., 2016), yet the additional surface areas from the elongate tail of *Archaeopteryx* are much larger. These additional flight surfaces likely contributed to the flight capabilities of these early birds and should be incorporated somehow into the functional landscape.

This raises the possibility that the real crux of the question “How do you make a flying bird?” may not be simply a question of what happened between nonavialan Paraves and Avialae, or even within early birds. Instead, this question may be more aptly directed toward the broader phylogenetic range between nonparavian and avialan taxa. Culminations of several overarching trends within theropods appear at Paraves: body size reduction (Carrano, 2006; Turner et al., 2012; Dececchi and Larsson, 2013; Lee et al., 2014), which is correlated with relative forelimb elongation (Benson and Choiniere, 2013; Dececchi and Larsson, 2013), pennaceous feather development and elongation (Foth et al., 2014), and changes to the pectoral girdle and enhanced range of motion (Turner et al., 2012). All these factors are prerequisites for powered flight and, as shown here, given the size range that many paravians occupy,

with these fundamental aspects of the bauplan in place, bridging the gap between flightless and flighted individuals is not a huge evolutionary step. In fact, it mirrors in many ways what is seen in juvenile birds as proposed previously by Dial and colleagues (Davis, 2005; Tobalske and Dial, 2007; Jackson et al., 2009; Heers et al., 2011, 2014, 2016) with the small body size and large wing areas helping to compensate for lower relative pectoral mass, assuming they are within the range of 8%–10% of total mass.

The real question is how this extreme evolutionary change started and what were the drivers within paravians that fostered it, since it is divorced from either the selective pressures that drove the previously mentioned long-term trends within theropods. Multiple scenarios, from wing-assisted incline running (Heers et al., 2014), stability flapping during prey capture (Fowler et al., 2011), thrust production to increase running speed (Burgers and Chiappe, 1999), to increasing leaping distance and/or height for prey capture (Cagle et al., 1983) have been suggested. These are all functionally and ecologically plausible and resemble behaviors seen in extant analogs. Although we do not as yet have any way to conclusively discern which of these behaviors, alone or in combination, influenced lineages within Paraves (but see Dececchi et al., 2016, for some insight into this issue), refocusing our investigations onto the multitude of small-bodied paravians may provide more insight to how dinosaurs tinkered at their functional limits before eventually conquering the air.

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