Ontogeny of aerodynamics in mallard ducks: comparative performance and developmental implications

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Wing morphology correlates with flight performance and ecology among adult birds, yet the impact of wing development on aerodynamic capacity is not well understood. Recent work using chukar partridge (*Alectoris chukar*), a precocial flier, indicates that peak coefficients of lift and drag (*C_l*, *C_d*) and lift-to-drag ratio (*C_l:C_d*) increase throughout ontogeny and that these patterns correspond with changes in feather microstructure. To begin to place these results in a comparative context that includes variation in life-history strategy, we used a propeller and force-plate model to study aerodynamic force production across a developmental series of the altricial-flying mallard duck (*Anas platyrhynchos*). We observed the same trend in mallards as reported for chukar in that coefficients of vertical (*C_V*) and horizontal force (*C_H*) and *C_V:C_H* ratio increased with age, and that measures of gross-wing morphology (aspect ratio, camber porosity) in mallards did not account for intraspecific trends in force production. Rather, feather microstructure (feather unfurling, rachis width, feather asymmetry and barbule overlap) all were positively correlated with peak(*C_V:C_H*). Throughout ontogeny, mallard primary feathers became stiffer and less transmissive to air at both macroscale (between individual feathers) and microscale (between barbs/barbules/barbicels) levels. Differences between species were manifest primarily as heterochrony of aerodynamic force development. Chukar wings generated measureable aerodynamic forces early (<8 days), and improved gradually throughout a 100-day ontogenetic period. Mallard wings exhibited delayed aerodynamic force production until just prior to fledging (day 60), and showed dramatic improvement within a condensed two-week period. These differences in timing may be related to mechanisms of escape used by juveniles, with mallards swimming to safety and chukar flap-running up slopes to take refuge. Future comparative work should test whether the need for early onset of aerodynamic force production
in the chukar, compared with delayed, but rapid, change in the mallard wing, leads to a limited repertoire of flight behavior in adult chukar compared with mallards.

Keywords: lift, drag, propeller, flight, bird, ontogeny, life-history

INTRODUCTION

The avian clade exhibits a broad array of wing morphologies and flight behaviors. Wing morphology varies among species and throughout development, playing a central role in life-history and juvenile survival (Dial et al. 2006; Jackson et al. 2009). Although adult morphology correlates with flight performance and ecology (e.g., Rayner, 1988), little is known about aerodynamic function of developing wings, particularly over the range of precocial to altricial birds (Tobalske and Dial, 2007; Heers et al. 2011). Birds which fly early in development are precocial fliers, where those which delay flight to adulthood are altricial fliers. The ontogenetic characteristics of feather and wing morphology differ markedly between precocial and altricial fliers (Nice, 1962), such that aerodynamics throughout ontogeny and into adulthood will likely contrast. In this study, we compare the acquisition of aerodynamic lift and drag production in mallard ducks (Anseriformes: *Anas platyrhynchos*, hereafter: “mallard”), which delay flight to the adult stage, with that recently reported for chukar partridges (Galliformes: *Alectoris chukar*, hereafter: “chukar”), which exhibit early flight capability within one week after hatching (Dial et al. 2006; Tobalske and Dial 2007; Heers et al. 2011).

Wing morphology is reported to affect steady-state aerodynamics during gliding (Withers, 1981). Surprisingly, though, significant changes in wing morphology (planform, leading-edge detail, camber, twist, aspect ratio) appear to have only minor effects upon the
aerodynamics of revolving wings, which emulate wing flapping during hovering or flight at very low advance ratios (Usherwood and Ellington, 2002a, b; Usherwood, 2009). Among insect and bird wings spanning Reynolds numbers (Re) from 1100 in mayfly (Ephemera vulgata) to 26000 in blue-breasted quail (Conturnix chinensis), there are no major differences in coefficients of vertical and horizontal force (C_V and C_H), or, using a frame of reference rotated to account for induced velocities, coefficients of lift (C_L) and drag (C_D) (Usherwood and Ellington 2002b). Profiles (polar diagrams) of C_V and C_H are also largely unaffected when rock dove (pigeon, Columba livia) wings are replaced with flat cardboard replicas (Usherwood 2009). These results suggest that details of morphology do not significantly affect force production per unit of wing area during hovering or very slow flight. Some exceptions to this pattern, however, include hummingbird (Trochilidae) wings at low angles of attack (α), which produce significantly more lift than flat-plate models (Altshuler et al. 2004), and recent work with pigeon wings where peak coefficient of lift (C_{L,max}) and the lift-to-drag ratio (C_L:C_D) is less with the wing in the posture of upstroke than when in downstroke (Crandell and Tobalske, 2011).

Recently, the ontogenetic development of wing and feather morphology has provided new insight into the relationship between wing design and flapping aerodynamics, at least within the limits of a propeller-force plate model. Heers et al. (Heers et al. 2011) studied a developmental series of chukar and demonstrated that feather properties and microstructure (flexural stiffness, asymmetry, number of barbicels and degree of barbule overlap) all correlate with C_{L,max} and C_L:C_D. In contrast, gross morphology of the wing (camber, aspect ratio, porosity) does not correlate with wing performance across age classes (Heers et al. 2011). This work, performed on the precocially-flying chukar, provides a foundation for the present study, in which we conduct an initial comparative test of the generality of the trends reported by Heers et
al. (Heers et al. 2011) using mallards, which have an alternative developmental trajectory. Unlike chukars, mallards do not develop a functional wing early in development.

Development of wing function is a crucial component of survival in flying birds, allowing for predator escape and novel foraging opportunities (Jackson et al. 2009). Chukar juveniles, for example, are capable of producing lift within one week of hatching as they use their wings to ascend slopes (wing-assisted incline running, WAIR, Tobalske and Dial 2007, Heers et al. 2011) and control aerial descents (Jackson et al. 2009). Their short, broad, highly cambered wings are implemented early in ontogeny for short, accelerative flapping behaviors that allow them to reach a refuge (Dial et al. 2006). At one-fifth the developmental period (20 days post hatching, d.p.h.), juveniles are capable of sustained flight, and although flight performance improves throughout ontogeny (~100 days), adult flight style changes very little (Dial et al. 2006). In contrast, immature birds of species with altricial wing development, such as the mallard, walk or swim to predator-free refuges. Anseriformes (waterfowl) are precocial in hindlimb-powered locomotion, but delay growth of the forelimbs until just prior to fledging (Stark and Ricklefs 1998). Waterfowl spend their ontogenetic period exploiting food-rich and predator-free ponds and rivers, using flight at the adult stage for long-distance seasonal migration in addition to burst-escape accelerations that are the hallmark of predator escape in non-migratory chukar (Tobalske and Dial, 2000).

Our goals, therefore, were to explore mallard ontogeny as part of a broader comparative test of the trends reported for chukar (Heers et al. 2011), and to evaluate wing and feather morphology and performance in relation to life-history strategy.

MATERIAL AND METHODS
We generally followed the methods of Heers et al. (2011) for the experiments and analysis; additional details, particularly regarding the morphology of chukar wings, are available therein.

Wing preparation and ontogenetic series

The mallard ontogenetic series began at 30 d.p.h., whereas the chukar series began at 8 d.p.h. (Heers et al. 2011), as these were the earliest stages of wing development for which our propeller and force-plate apparatus (Crandell and Tobalske, 2011, Fig. S1) could resolve forces when the wings were spun at *in vivo* angular velocities. Wing stages were selected based on transitions in feather morphology and wingbeat kinematics beginning with the emergence of pinfeathers, progressing through barb unfurling, and ending with an adult wing (Tables 1 and 2). Two right wings were examined for each ontogenetic stage.

Wings were removed at the shoulder and pinned and taped to dry. The posture of the wings mimicked *in vivo* spread at mid-down stroke, determined using high-speed video (1000 Hz; shutter speed 1/4000 s; Redlake PCI-2000, Redlake MASD LLC, San Diego, CA, USA) of each species during wing-assisted incline running (WAIR) at 65° for chukars (Dial et al. 2008; Jackson et al. 2009) and during descending flight for mallards. These behaviors (WAIR, descending flight) were selected because they could be achieved by birds of all ages. A brass rod (1.5 to 5 mm in diameter according to wing size) was inserted into a pre-drilled hole in the head of the humerus. The attachment was reinforced using epoxy cement. The rod served to mount the wing on the shaft of a motor (section 2b below) and provided counterbalance.

Propeller apparatus and force recordings

All wings were mounted ventral side up, with the leading edge of the wing parallel to the horizontal plane of the force plate. The propeller apparatus-force plate assembly was the same
for all spin trials (Figure S1) except for the motor used. Mid-experiment, we were compelled to
increase the torque capacity of the motor to accomplish the mallard measurements. We used a
NEMA 23 brushless DC motor (Anaheim Automation, Inc., Anaheim, CA, USA, Model
BLWR232S-36V-4000, Luminary Micro, Texas Instruments, Dallas, TX, USA, LM3S8971
BLDC Motor controller) for chukar wings and a NEMA 34 stepper motor (Anaheim
Automation, Inc., 34W214D-LW8; DCL 601USB, MBC 12101 and PSA 40V8A driver and
power supply, SMC60WIN v. 2.01 software ) for mallard wings.

The motors were attached to a custom-built force plate (Bertec Corp., Columbus, OH,
USA) to measure vertical force and horizontal torque about the z-axis (Usherwood, 2009). A
shield housing (cowling) isolated the force plate from air velocities induced by upwash from the
spinning wing. Resonant frequency for the plate-motor assembly (Fig. S1) was 220 Hz. Voltage
output from the force plate was amplified (1-100x, depending upon wing size) using a Bertec
model M6810 amplifier. Data were imported into a PC computer using an ADInstruments
PowerLab (ADInstruments, Inc., Colorado Springs, CO, USA) 8SP A/D converter sampling at
1000 Hz, and recorded using Chart v5.2 (Fig. S2; ADInstruments Inc., 1 Hz low-pass digital
filter). Voltages were transformed using known conversions of 10000 mN/V for force and 800
mNm/V for torque.

Spin trials

For each age-class, in vivo angular velocity, averaged over down stroke (Table 1), was
determined using high-speed video and converted to revolutions per minute (RPM) for driving
the propeller (Table 1). We calculated Reynolds number (Re) using average wing chord and
wingtip velocity (Ellington, 1984). Angular velocities for chukar were obtained during bouts of
65° WAIR (Jackson et al. 2009) and, for mallards, during descending flight. Due to uncertainty
on whether such behaviors are directly comparable, we tested intermediate-age chukar and
mallard wings at double and half RPM. Consistent with Usherwood (Usherwood 2009), RPM
did not significantly affect $C_V$ and $C_H$, particularly over the in vivo range of $\alpha$.

We performed spin trials over a range of $\alpha$ from -20° to 90° in ~10° increments.

Geometrically, $\alpha$ was measured relative to the plane of rotation using reflective markers placed
on the feathers overlying the wrist and on the trailing edge of the first secondary. Wings
deformed under aerodynamic loading, and herein we report the “active” $\alpha$ recorded during
spinning. Spinning wings were videotaped using a Photron SA-3 camera (Photron USA Inc.,
San Diego, CA, USA), with 1024 x 1024 pixel resolution, sampling at 1000 Hz with a shutter
speed of 1/5000 sec (Photron PFV v.3.20). We estimate $\alpha$ measurement error at ±1°. We used
high-speed video frames to calculate change in $\alpha$ ($\Delta \alpha$) between “active” $\alpha$ during spinning and
“static” $\alpha$ prior to spinning.

In an initial attempt to reveal structural mechanisms responsible for ontogenetic changes
in morphology and aerodynamic force output, we measured primary-feather stiffness following
the methods of Heers et al. (Heers et al. 2011) (7th primary for D40 and D60 birds, N=2 for each
age class). Here, flexural stiffness was determined as:

$\text{flexural stiffness} = EI = F_a l^3/3\delta$  \hspace{1cm} (3)

where $E$ is Young’s modulus, $I$ is the second moment of area, $F_a$ is the applied force, $l$ is the
effective beam length (70% of feather length) and $\delta$ is feather displacement (<10% of $l$) (Combes

As a check upon our methods, and to further test the functional contribution of feather
structure in the juvenile wings, replica chukar and mallard wings were constructed and their
aerodynamic properties evaluated. The flat, artificial wings were made of two pieces of
cardboard, glued together using epoxy and reinforced with a 1.4-mm diameter brass rod inserted between the cardboard sheets. Thickness in the region of the rod was 2.08 mm; elsewhere thickness was 0.68 mm. The wings had the same outline as chukar day 8 and mallard day 30 wings, and the wings were spun at the same angular velocities as appropriate for these two age classes (Table 1). Additionally, $C_V:C_H$ as a function of $\alpha$ was compared against an idealized flat plate without leading-edge suction (i.e., with flow separation). In an idealized flat plate, which has a sharp leading edge and high angle of incidence, aerodynamic force acts perpendicular to the wing surface ($C_V:C_H=1/\tan(\alpha)$; Dickinson, 1996) as opposed perpendicular to direction of travel.

Average lift and torque measurements for wings were captured over 10 seconds of steady-speed rotation (Fig. S2). We specifically avoided sampling the transient phases at the start and stop of motor activity, and our plateau phases therefore did not exhibit the same level of transient change as typical of the ‘early’ or ‘steady’ phases in Usherwood and Ellington, 2002a. The drag produced by the counterbalancing rods during these trials was subtracted (Usherwood, 2009; Heers et al. 2011).

Vertical and horizontal force coefficients ($C_V$ and $C_H$) were determined from the force plate output. Vertical force ($F_V$) was measured directly along the z-axis and horizontal force ($F_H$) was determined from the torque ($Q$, Nm) about the z-axis. Force coefficients were calculated from these measures following Usherwood and Ellington 2002a. $C_V$ was calculated as:

$$C_V = \frac{2F_V}{\rho S_2 \Omega^2}$$  \hspace{1cm} (1)$$

where $\rho$ is air density (1.07 kg m$^{-3}$, Missoula, MT, USA), $S_2$ is second moment of area (m$^4$) and $\Omega$ is angular velocity of the wing (rad/sec). $C_H$ was calculated as:
\[ \frac{C_H}{Q} = \frac{2}{\rho S_3 \Omega^2} \]

where \( S_3 \) is third moment of area (m\(^5\)). Previous research has included coefficients of lift \((C_L)\) and drag \((C_D)\) computed using a rotated frame of reference that takes into account estimated induced velocities at blade elements along the span of the rotating wing (Usherwood and Ellington, 2002a, b; Usherwood, 2009; Heers et al. 2011; Crandell and Tobalske, 2011). Because aspect ratio should have an effect upon lift distribution and local induced velocities, aspect ratio may be confounded with \( C_L \) and \( C_D \), so, for our present comparative analyses, we use only \( CV \) and \( CH \).

We calculated \( CV \) and \( CH \) using second and third moments of wing area (Table 1), respectively. For each wing, 100-point spline-interpolation curves were fitted for \( CV \) and \( CH \) versus active \( \alpha \) (-15° to 80°; IGOR Pro v.6.12, Wavemetrics Inc., Portland, OR, USA). We used the fitted curves to compute means for the two wings for each age class. We used the averaged values to produce polar diagrams of \( CV \) as a function of \( CH \) and \( CV:CH \) ratio as a function of \( \alpha \).

Wing morphology and feather microstructure analysis

We measured aspects of wing morphology (length (m), area (m\(^2\)), second and third moments of area (m\(^4\), m\(^5\)) and wing porosity (%) (Heers et al. 2011)) using a digital camera to photograph the dorsal view of a dried wing. We analyzed these images using ImageJ (v1.42 National Institutes of Health, Bethesda, MD, USA) and custom m-files in MatLab R2010a (MathWorks, Natick, MA, USA). We determined maximum camber (dimensionless) by dividing maximum wing height at the wrist by average wing chord (Heers et al. 2011). Wing height was measured as the highest point of curvature with the wing set ventral side down on a flat table. Maximum height was consistently at the wrist. Camber values are likely inflated relative to camber for a blade element centered on the wrist due to long-axis curvature of the
whole wing, which was not taken into account for the measurement. Aspects of feather microstructure were determined for the mallard at days 45, 60 and post-molt adult. Consistent with Heers et al. (Heers et al. 2011), we removed the 10th primary feather for light scanning (HP Photosmart scanner, Palo Alto, CA, USA, at a resolution of 236 pixels cm\(^{-1}\)) to determine feather unfurling (%), asymmetry (%) and rachis width (mm). The feathers on the wings of day 30 mallards were downy, so quantitative comparisons were not feasible. We obtained scanning electron micrographs (Hitachi S-4700 cold field emission SEM (Hitachi High Technologies America Inc., Pleasanton, CA, USA) at the tip and 25% proximal from the tip of the feather to determine barbule overlap (%) and barbicel/barbule ratios (dimensionless). For further comparison, a post-molt, adult feather was obtained from the University of Montana, Philip L. Wright Zoological Museum.

Transmissivity

Based upon morphology of the wings (Heers et al. 2011; Figs. 6, 7), we hypothesized that wing transmissivity (Müller and Patone, 1998) would be at least partially responsible for relatively poor aerodynamic performance in juvenile wings. Here we define two scales of transmissivity, or air movement perpendicular to the wing surface, from underside to upper side. Macro-scale is considered to be air movement between feathers; micro-scale is considered to be air movement between barbs, barbules and barbicels. We used particle image velocimetry (Spedding et al. 2003; Tobalske and Dial, 2007) to measure macro-scale transmissivity in duck wings at D40 and D60 and our cardboard D30 model, and we used a vacuum-driven flow circuit (Müller and Patone, 1998) to measure micro-scale transmissivity in the D40 and D60 wings. Macro-scale transmissivity was determined by placing wings in a wind tunnel (details of tunnel in Tobalske et al. 2005) and using particle-image velocimetry (PIV) to reveal near-field
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flow about the wing surface (Spedding et al. 2003; Warrick et al. 2005; Tobalske and Dial, 2007; Tobalske et al. 2009). We measured the cardboard wing chord at 2/3 point on the wing; primaries 1-3 were measured in the D40 and D60 bird. Wings were placed perpendicular to air flow ($\alpha = 90$ degrees). Air speed in the wind tunnel was matched to the wing speed of primaries 1-3 during spinning trials, which meant that free-stream velocity was 3.6 m s$^{-1}$, 3.3 m s$^{-1}$ and 8.8 m s$^{-1}$ for the cardboard model, D40 wing and D60 wing, respectively. We obtained 50 images and averaged velocity to then compute vorticity from the averaged flow field. Our interrogation area for sampling velocity was a square centered on the wing or primaries, with side lengths of the square equal to 75% of the width of the chord (cardboard model; D40 wing) or the width from the edge of primary 1 to the edge of primary 3 (D60 wing). The sampled areas were immediately in front of and behind the wing, outside of the shadow created by the wing that obstructed the laser light.

For PIV, we used a LaVision GmBH system with DaVis 7.1 software (Goettingen, Germany), a Flowmaster 1376_1040 pixel digital camera (Goettingen, Germany) sampling at 5 Hz and a 50 mJ dual-cavity pulsed Nd:YAG laser (New Wave Research Inc., Fremont, CA, USA). We seeded the air with particles of olive oil ($<1$ $\mu$m in diameter) generated at a rate of 7x10$^{10}$ particles s$^{-1}$ using a vaporizer fitted with a Laskin nozzle. We placed the camera perpendicular to the planar ($\sim$3 mm thick) illumination field. To calculate particle velocity, we used cross-correlation of paired images with an elapsed time between images ($\Delta t$) of 250–400 ms to give $\sim$10 pixel particle separation in the regions of greatest velocity. We employed an adaptive multipass with an initial interrogation area of 64x64 pixels and final area of 16x16 pixels with 50% overlap. Vector fields were post-processed using a median filter (strong removal if difference relative to average $>2$ the r.m.s. of neighbors and iterative reinsertion if $<3$ the
r.m.s. of neighbors), removal of groups with <5 vectors, fill of all empty spaces by interpolation and one pass of 3x3 smoothing. We estimated minimum error in velocity measurements to be 5.0±0.5% including contributions due to a correlation peak of 0.1 pixels, optical distortion and particle–fluid infidelity (Spedding et al., 2003).

Air movement through an individual feather, defined as micro-scale transmissivity ($T$; $m^3 s^{-1} N^{-1}$), was measured using a closed-line flow circuit, designed to measure the pressure differential across feather sections at the barb-barbule-barbicel level (Müller and Patone, 1998). A shop-vac Pro vacuum (Shop-Vac Corp., Williamsport, PA, USA) provided suction in the circuit; flow rate was regulated using a Brooks Flowmeter (1355-00C1 AAA, Emerson Electric Co., Hatfield, PA, USA) and pressure across the feather was measured using a Setra Datum 2000 Pressure Transducer (2239 Manometer, Setra Systems, Boxborough, MA, USA).

Transmissivity was calculated as:

$$T = Q/\Delta PA$$

where $Q$ is air flow in Lm$^{-2}$, $\Delta P$ is the pressure differential across the feather section in Pascals (Nm$^{-2}$) and $A$ is area in $m^2$. Transmissivity is therefore a variable describing the degree to which air passes through a section of feather, regardless of the pressure differential or area of feather sample (Muller and Patone, 1998). Feather samples were taken from the inner vane, 10% inward from the feather tip in the second primary of D40 and D60 mallards and also in a tertial feather of D60.

**Statistical analysis**

We tested for correlations between peak $C_V:C_H$ and variables in mallards describing whole-wing morphology using values for each individual within each age class. To describe whole-wing deformation during spin trials, regressed $\Delta \alpha$ as a function of resultant force.
coefficient \( \text{CR} = \text{Cv} + \text{Ch} \) using least-squares regression. Statistical analyses were performed using Excel (v2010, Microsoft, Inc., Redmond, WA, USA) and IGOR Pro (v.6.12, Wavemetrics Inc., Portland, OR, USA). Throughout, we report means ± SD except in graphs where we report mean and range (i.e., min-max for \( n = 2 \) birds per age class).

RESULTS

Mallards reached an average terminal mass of ~1300g (Dial 2010) over a 60 d.p.h. ontogenetic period, whereas previous work has shown that fully-grown chukar average ~600g and develop for ~100 d.p.h (Tobalske and Dial, 2000; Dial et al. 2006; Jackson et al. 2009).

Peak vertical coefficient \( (C_{V_{\text{max}}}) \) and maximum \( C_{V}:C_{H} \) were observed to be roughly similar at comparable stages of development, and a marginally higher peak in the adult mallard compared with the adult chukar appeared insignificant given the large variation between conspecifics in the same age class. Consistent with the patterns previously reported for \( C_L \) and \( C_D \) in chukar (Heers et al. 2011), mallards exhibited an ontogenetic increase in \( C_{V_{\text{max}}} \) and \( C_{V}:C_{H} \) ratio (Figs. 1-4).

Furthermore, as in Heers et al. (2011), we observed significant correlations between peak \( C_{V}:C_{H} \) and four measures of feather microstructure including feather unfurling, rachis width, feather asymmetry, and barbule overlap (Figure 4; Table 2), whereas there was no significant effect of camber, aspect ratio or wing porosity \((0.37 < P < 0.91)\) (Tables 1 and 2).

Comparative aerodynamic performance

In both species, peak \( C_{V}:C_{H} \) increased with age and was generated at progressively lower \( \alpha \) (Figs 1 and 2). Day 8 chukar wings produced more horizontal force (“drag”) compared with vertical force \((\text{maximum} \ C_{V}:C_{H} = 0.88; \ \alpha = 30)\), whereas day 10 chukar wings were capable of
producing more vertical than horizontal force (maximum $C_V:C_H = 1.44; \alpha = 37^\circ$; Figure 1A, 2A) and by the final stage of chukar wing development (day 100), maximum $C_V:C_H$ increased to 4.0 (Figure 2, 3). Day 30 mallard wings were practically incapable of vertical force generation: even at maximum $C_V:C_H$, horizontal force outweighed vertical force seven-fold ($C_V:C_H = 0.64$).

Between day 30 and day 45, peak $C_V:C_H$ improved from 0.64 to 1.46. Aerodynamic performance culminated at the adult condition with wings capable of producing $C_V:C_H_{\text{max}} = 5$, 40% more vertical than horizontal force at $\alpha = 0^\circ$ ($C_V:C_H_{0^\circ} = 1.40$), and $C_V_{\text{max}} > 2$ (at $\alpha = 31^\circ$; Figure 1b, 4c). It is worth noting that the day 60 mallard has not gone through a molting period, where the day 100 chukar has. Post-molt feathers have greater aerodynamic performance in chukar (Heers et al. 2011), suggesting that post-molt feathers in mallards might have even greater performance than that reported here for day 60 birds. In vivo wing kinematics (from the initial videos taken to determine wing angular velocities), suggest $\alpha$ is not optimized for maximum $C_V:C_H$ or $C_V_{\text{max}}$, but rather spans a range of $\alpha$ values. Both $C_V:C_H$ and $C_V_{\text{max}}$ are, therefore, important metrics in comparing aerodynamic performance between species and over the course of ontogeny.

Our cardboard models of 8 day chukar wings and 30 day mallard wings exhibited higher $C_V_{\text{max}}$ and peak $C_V:C_H$ as well as lower minimum $C_H$ compared with wings from real birds (Figs. 1 and 2). For the bird wings, $C_V:C_H < 1.5$, whereas $C_V:C_H = 3.15$ at $\alpha = 17$ deg in the duck cardboard model and $C_L:C_D = 2.92$ at $\alpha = 18^\circ$ in the chukar cardboard model. Minimum $C_H = 0.10$ ($\alpha = 8^\circ$) in the duck cardboard model and 0.07 ($\alpha = 10^\circ$) in the chukar cardboard model, whereas $C_H \sim 0.5$ at $\alpha = 0^\circ$ in the youngest bird wings (Fig. 1). When compared with a theoretical flat plate (Dickinson, 1996), 50 day wings and older exhibited slightly higher $C_V:C_H$...
ratios when $\alpha > 15^\circ$, but differences were generally within the range exhibited between individuals of a given age class (Fig. 2).

Considerable variation was apparent between the two wings within each age class, although this variance was proportionally greater for the wings from the youngest birds and tended to decrease with age (Fig. 3). We attribute this variance to differences in morphology of the dried wings (note SD’s Tables 1 and 2), as well as error introduced with the lower signal-to-noise ratio inevitable when measuring smaller forces from the wings of the youngest birds (Fig. S2).

A stark contrast was apparent in the timing and trajectory of aerodynamic development between mallards and chukar. Chukar show early, gradual improvements (Heers et al. 2011), whereas mallards show delayed, dramatic shifts in aerodynamic capacity (Figure 4). The earliest stage at which chukar and mallard wings were capable of producing lift that was measurable with our force-plate apparatus was day 8 and 30, respectively (Figure 4). More-sensitive flow measurements reveal that wings from younger (day 4) chukar can generate lift (Heers et al. 2011), but we did not attempt such measurements for mallards in the present study. For chukar, day 8 corresponds well with the in vivo onset of lift during controlled flapping descent and WAIR (Tobalske and Dial, 2007; Jackson et al. 2009). However, flapping-descent experiments with mallards (Dial 2010) reveal that they do not produce significant lift in vivo until day 45. From day 8 and day 45, respectively, the time period required to reach the adult-wing condition was 90 days for the chukar and 15 days for the mallard wings (Heers et al. 2011; Fig. 4).

Feather morphology changed consistently with increasing age in mallards (Table 2; Fig. 5). Feather unfurling increased from 74 % to 99%, rachis width (relative to adult condition) increased from 40% to 100%, feather asymmetry increased from 3 to 5, barbicels / barbule
increased from ≤ 1 barbicel to between 1 and 2 barbicels (post-molt adult: > 5), and barbule overlap increased from 74% to 97% (post-molt adult: 109±11%). In contrast, although absolute measures of length and area of the wings obviously increased with age (Fig. 1, Table 1), our measures of gross morphology that do not contribute to calculations of \( CV \) and \( CH \) (namely \( AR \), camber and wing porosity) did not vary in a consistent manner with age in mallards (Table 1, Figure 1), as previously reported for chukar (Heers et al. 2011).

**Flexibility and transmissivity**

Our direct measures of flexural stiffness (\( EI \)) revealed that feather stiffness for primary 2 increased dramatically with age. For day 40 mallard, \( EI = 9.3 \times 10^{-5} \text{ Nm}^2 \) and for day 60, \( EI = 9.18 \times 10^{-3} \text{ Nm}^2 \), indicating day 60 is much stiffer than day 40. These values of \( EI \) were on par with day 20 and day 100 chukar (Heers et al. 2011). Regressing \( \Delta \alpha \) as a function of \( CR \), we observed wing and feather deformation during spin trials increased throughout ontogeny (\( \Delta \alpha = 7.6*CR - 7.8 ; r = 0.79 ; p<0.01; \text{ d.f.} = 1.9 \)). Although the older feathers are stiffer, they deformed more during spin trials, likely due to higher \( CR \). In general, spinning wings deformed under aerodynamic loading by twisting along the long axis such that the absolute value of \( \alpha \) decreased (i.e, negative initial \( \alpha \) became less negative; positive initial \( \alpha \) became less positive). For example, the average \( \Delta \alpha \) among all subjects and age classes of mallards with an active (spinning) \( \alpha \sim 45 \text{ deg} \) was \(-4 \pm 5 \text{ deg} \) relative to the static \( \alpha \).

Whole-wing transmissivity decreased throughout ontogeny. Average air velocities perpendicular to the day 40 wing were \( 2.5 \pm 0.3 \text{ m s}^{-1} \) leading into the wing and \( 1.2 \pm 1.3 \text{ m s}^{-1} \) behind the wing, indicating that flow passes through the individual feathers and leaves a highly variable flow field behind the wing (Fig. 6). In contrast, flow in the vicinity of the day 60 wing (4.8 \( \pm 1.4 \text{ m s}^{-1} \) incurrent and \(-0.6 \pm 0.5 \text{ m s}^{-1} \) in the wake) indicates recirculation of air in a
vortex-formation region, with feathers acting together like a flat plate (Vogel, 1996). Our actual flat-plate, cardboard replica exhibited a similar flow pattern and velocity distribution as the day 60 wing, with incurrent velocity in front of the cardboard wing at 2.1 ± 0.8 m s⁻¹ and velocity behind the model at -0.2 ± 0.1 m s⁻¹).

Microscale transmissivity (T) also decreased throughout ontogeny. Within the vacuum-driven flow circuit, average transmissivity at flow rates (Q) > 0.49 was 2.6 x 10⁻⁴ m³ s⁻¹N⁻¹ for day 40 primary 2 and 1.4 x 10⁻⁴ m³ s⁻¹N⁻¹ for day 60 primary 2 (Figure 6). Smaller numbers indicate that less air passes through the section of feather, so the day 60 primary was much less transmissive than the day 40 primary. For comparison, the day 60 tertial had higher average T than either primary feather: 1.15 x 10⁻³ m³ s⁻¹N⁻¹. These values of T in the day 40 and day 60 birds are within the range of values for T reported for feathers in the European kestrel (Falco tinnunculus) (Müller and Patone 1998).

**DISCUSSION**

The general trends we observed in mallards for the development of aerodynamic forces and feather morphology were consistent with those previously reported for chukar as coefficients of lift and drag (Heers et al. 2011), supporting a conclusion that feather microstructure probably has a more dramatic effect than gross wing morphology upon wing aerodynamics during spinning (Table 2; Fig. 5). Cardboard models with the same outline as juvenile bird wings generated higher $C_{V,max}$ and $C_V:C_H$, and lower minimum $C_H$, which further emphasizes an important role of feather structure upon wing performance. Overall, our results are consistent with an interpretation that whole-wing morphology has scant influence upon performance during spinning trials (Usherwood and Ellington, 2002a,b; Usherwood, 2009; Heers et al. 2011) unless
wing posture is radically altered as during upstroke versus downstroke (Crandell and Tobalske, 2011).

Our results support a recommendation that, for take-off and slow flight at low advance ratios, resultant force coefficients ($C_R$) are appropriately modeled as being perpendicular to the plane of a bird’s wing rather than perpendicular to the direction of wing translation (Dickinson, 1996). The expectation for a translating flat plate is that $C_R$ is perpendicular to the plane of the plate when $\alpha > 15$ deg, potentially, but not necessarily, associated with formation of a leading-edge vortex (LEV) (Dickinson, 1996). Wings from older birds (day 50 – 60) exhibited slightly higher values of $C_V: C_H$ compared with values for such a theoretical flat plate model, particularly at $15 \text{ deg} < \alpha < 45$ deg (Fig. 2), but the high variability between individuals in each age class suggests it is best, at present, to conclude rough agreement with predictions from a flat-plate model.

In addition to corroborating general trends in chukar (Heers et al. 2011), our study offers novel observations about potential aerodynamic mechanisms that can account for the trends as well as new insight into the timing of wing development. Macro and micro transmissivity both decreased with age in mallards (Figure 6, 7). We therefore conclude that stiffer feathers and wing impermeability to air creates a wing capable of generating greater aerodynamic force across a large range of $\alpha$ (Figure 2, 3). This pattern is consistent with data from the fossil record, which suggests that barbules and barbicels (ie, closed pennaceous feathers, Prum 1999) evolved in theropods that were beginning to accumulate skeletal features associated with flight capacity. Feather maintenance (preening) likely functions to realign feather overlap (Clumpner 1990), as well as interdigitate barbicels (hooklets) at the microscopic level, and thus may be important for reducing transmissivity. As all aspects of development are intercorrelated (Table 1, 2), a future
challenge will be to isolate aspects of feather structure to test the relative contribution of
variables such as flexural stiffness or barbule overlap upon macro and micro transmissivity.
Likewise, it will be necessary to isolate macro and microtransmissivity to understand their
effects upon aerodynamic performance.

The timing of wing development differs dramatically between mallards and chukar
(Heers et al. 2011; Fig. 4). This appears to be due to the mechanisms juveniles use for escape,
and it may reflect different selective pressures early in life history. Although precocial in their
early locomotor ability to run and swim, the developmental trajectory of the mallard forelimb
parallels that of altricial birds. Developing mallards do not use flight for survival during their
vulnerable period as juveniles; instead they swim to a refuge. Wing maturation initiates late in
ontogeny and is condensed to a brief window of ~15 days (Fig. 4). In contrast, it is likely that
strong selective pressures (e.g. predation) have acted historically and are currently acting on
terrestrial chukars to cause them to use their wings to produce aerodynamic force prior to
attaining mature size. Juvenile chukars beginning at ~7 days will use their wings to produce lift
and help them escape as they run up slopes; this is well before they can support their weight in
flight (Tobalske and Dial, 2007; Jackson et al. 2010).

Might the differences between species in timing of wing development be related to their
adult flight styles? As adults, mallards exhibit impressive capacity for burst take-off, but they
are also highly migratory (Cooke 1933); in contrast, adult chukar use high-power, burst takeoff
for escape and then immediately return to the ground to run for cover (Tobalske and Dial, 2000).
It has been suggested that an inherent tradeoff exists between the functional maturity of
structures and the rate of morphological development (Carrier, 1996; Starck and Ricklefs 1998).
As a result of ontogenetic canalization (Frazzetta 1975; Carrier 1996), it may be that wing
morbidity and aerodynamic capacity in adults is constrained by early onset of aerodynamic function in juveniles. Future research should seek to test this idea in a broader phylogenetic context, as interpretation of two-species comparisons (i.e., mallard vs. chukar) necessarily requires extreme caution (Garland and Adolph, 1994) and is inadequate for testing for adaptation or revealing patterns of transformation (Gould and Lewontin, 1979; Lauder, 1981).

The Galliformes may be an excellent phylogeny within which to test the “canalization” hypothesis that early life history has driven adult morphology and behavioral repertoire. Some species within the Galliformes migrate moderate distances (e.g., white-tailed ptarmigan, Lagopus leucurus), have wings of relatively high AR as well as darker pectoralis muscles (presumably with higher oxidative capacity). This is in contrast with non-migratory species in the clade such as the chukar that appear to use flight solely for take-off escape from predation risk (Drovetski, 1996; Tobalske and Dial, 2000).

**Future directions**

Certainly live animals are ideal models for measuring aerodynamic performance, because natural wing flexibility and neuromuscular control of wing movements are far more complex than simple rotation of a dried wing about a fixed shaft. However, since live animals are not suited for measuring performance outside the envelope they will willingly perform, it has been necessary to remove kinematic and neuromuscular variables so that wing form and function may be measured directly. Within this study, wing shape was based off a kinematic analysis of flight in the laboratory and represented standing take-off, vertical flight or slow flight with low advance ratio. At best, the wing posture was relevant to mid-down stroke during flapping flight.

Kinematics of flapping flight are complex, with long-axis rotation of the wings and variation in camber and twist through the wingbeat (Oehme 1971, Tobalske et al. 2007). It is
known from robotic models that unsteady aerodynamics contribute significantly to the forces produced during hovering and slow flight (Ellington et al. 1996; Dickinson et al. 1999; Lehmann, 2004). Recent work using flapping insect wings (Mountcastle and Daniel, 2009) and computational fluid dynamics (Young et al. 2009) indicates that wing flexibility also has a significant effect upon aerodynamic function. In light of this, it is noteworthy that increasing force coefficients caused greater deformation of the whole wing during spinning (i.e., $\Delta \alpha$ had a positive effect upon $C_R$), suggesting that aeroelasticity may have deformed the more-developed wings in a manner that increased $C_V:C_H$ ratio (Fig. 2).

Deformation caused a decrease in the absolute value of active $\alpha$ compared with static $\alpha$, and this has implications for control of flight surfaces. For example, our results indicate a bird experiencing increased aerodynamic loading on its wings would experience aerodynamic damping of $\Delta \alpha$, which may, therefore, represent a form of passive stability. Increased loading might be initiated passively, due to shifts in wind velocity from turbulence (Combes and Dudley, 2009) or incurrent velocity during maneuvering; Hedrick et al. 2009). Alternatively, increased loading may occur actively, using a muscle such as the supracoracoideus to supinate the wing (Poore et al. 1997; Tobalske and Biewener, 2008).

Overall, then, an important challenge for understanding the effects of dynamic changes in morphology on aerodynamic performance and wing control will be to compare our data representing mid-wing translation with observations of near-field aerodynamics from live animals through the entire wingbeat cycle (e.g. Warrick et al. 2009).

**LIST OF SYMBOLS AND ABBREVIATIONS**

$A$ cross-sectional area
<table>
<thead>
<tr>
<th></th>
<th>Symbol</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>$C_D$</td>
<td>coefficient of profile drag</td>
</tr>
<tr>
<td>2</td>
<td>$C_H$</td>
<td>coefficient of horizontal force</td>
</tr>
<tr>
<td>3</td>
<td>$C_L$</td>
<td>coefficient of lift</td>
</tr>
<tr>
<td>4</td>
<td>$C_{L_{\text{max}}}$</td>
<td>maximum coefficient of lift</td>
</tr>
<tr>
<td>5</td>
<td>$C_R$</td>
<td>coefficient of resultant force</td>
</tr>
<tr>
<td>6</td>
<td>$C_V$</td>
<td>coefficient of vertical force</td>
</tr>
<tr>
<td>7</td>
<td>d.p.h.</td>
<td>days post hatching</td>
</tr>
<tr>
<td>8</td>
<td>$EI$</td>
<td>flexural stiffness</td>
</tr>
<tr>
<td>9</td>
<td>$E$</td>
<td>Young’s modulus</td>
</tr>
<tr>
<td>10</td>
<td>$F_a$</td>
<td>applied force</td>
</tr>
<tr>
<td>11</td>
<td>$I$</td>
<td>second moment of area</td>
</tr>
<tr>
<td>12</td>
<td>$l$</td>
<td>effective beam length</td>
</tr>
<tr>
<td>13</td>
<td>$Re$</td>
<td>Reynolds number</td>
</tr>
<tr>
<td>14</td>
<td>$T$</td>
<td>micro-scale transmissivity</td>
</tr>
<tr>
<td>15</td>
<td>$U$</td>
<td>wing velocity</td>
</tr>
<tr>
<td>16</td>
<td>$U_r$</td>
<td>local air velocity</td>
</tr>
<tr>
<td>17</td>
<td>$\alpha$</td>
<td>active (aerodynamically loaded) angle of attack</td>
</tr>
<tr>
<td>18</td>
<td>$\delta$</td>
<td>feather displacement</td>
</tr>
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</table>

ACKNOWLEDGEMENTS
We sincerely thank K. Dial, B. Jackson, D. Carrier and D. Bramble for their assistance in developing, executing and editing this study. We are also grateful to P. Little who assisted in conceptualizing, engineering and performing the micro-transmissivity experiment. Two anonymous reviewers provided helpful comments to the manuscript. Supported by NSF grants IOS-0923606 and IOS-0919799 to B.W.T.

Figure legends

Figure 1. Polar traces of vertical force coefficient ($C_V$) and horizontal force coefficient ($C_H$) for an ontogenetic series coupled with dorsal profiles of wings from (A) chukar partridge (Alectoris chukar) and (B) mallard (Anas platyrhynchos). $C_V$ and $C_H$ were measured at angles of attack ($\alpha$) from -15° to 80°. Symbols refer to $\alpha = 0°$ (circles), maximum $C_V:C_H$ (squares, $\alpha$ indicated) and maximum $C_V$ (triangles, $\alpha$ indicated). Axes are on same scale to aid comparison. Solid, colored traces are means from N = 2 birds per age class, with classes beginning at the earliest age force readings could be resolved and ending with adult wing. Grey dashed lines are from flat cardboard models of the youngest chukar and mallard (N = 1 per species). 5-cm scale bar is for wing images.

Figure 2. Lift-to-drag ratio ($C_V:C_H$) over range of angle of attack ($\alpha = -15°$ to 80°) from (A) chukar partridge (Alectoris chukar) and (B) mallard (Anas platyrhynchos) ontogenetic series (N = 2 birds per age class). Grey dashed lines are from flat cardboard models of the youngest chukar and mallard (N = 1 per species). Solid black line represents theoretical flat plate. Axes are at same scale for comparison between wing types. Lines and same-color shaded region represents mean, minimum and maximum.
Figure 3. Variability between wings (N= 2 per age class) for coefficient of lift ($C_L$, left column) and coefficient of drag ($C_D$, right column) as a function of angle of attack A and B = chukar, day 8; C and D = chukar, adult; E and F = mallard, day 30; G and H = mallard, day 60. Red and blue indicate individual wings; green indicates mean.

Figure 4. Ontogenetic trends between chukar and mallards at different points along the polar curves. (a) Change in $C_V:C_H$ at $\alpha = 0^\circ$. (b) Maximum $C_L:C_D$, $\alpha$ indicated in Figure 1, 2. (c) Maximum $C_V$, $\alpha$ indicated in Figure 1. Note the characteristic trend that chukar wing function initiates early and gradually improves throughout ontogeny, where mallard aerodynamic capacity is delayed to a brief window of maturation just prior to fledging.

Figure 5. Ontogenetic trends in mallard feather microstructure. Note number of barbicel hooklets and overlap between barbules. Scale bar 100µm. Images magnified 500X. See Heers et al. (Heers et al. 2011) for comparable images from chukar.

Figure 6. Macro-scale transmissivity in duck wings and a cardboard model as measured using particle image velocimetry. (A) Cardboard model of D30 wing, with black outline revealing cross-section of wing. (B) Day 60 wing, with three primaries (P1, P2 and P3) isolated to permit observation of flow local. (C) Day 40 wing, with close view of P1, P2 and P3. Red boxes in A and B indicate comparable size of interrogation area used for C. White vectors represent velocity (m s-1) and background colors represent vorticity (rad s-1). Areas in the vicinity of
feathers in B and C were masked because shadows caused by other feathers precluded measurements of local velocity.

Figure 7. (a) Micro-scale transmissivity showing flow rate (Q) as a function of $\Delta P$. The slope indicates conductance, and conductance per unit area is transmissivity. (b) Transmissivity as a function of Q. The figure labeled "transmissivity" shows flow rate (Q) as a function of $dP$ in the top panel; this is for direct comparison with Muller and Patone's figure 3. The slope indicates conductance, and conductance per unit area is transmissivity. The lower panel shows transmissivity as a function of Q.

Figure S1. Experimental setup of propeller-force plate apparatus. Several motors were interchanged (see text) to spin a single wing-mount over both chukar and mallard ontogenetic series at in vivo speeds converted to RPMs (Table 1). Force and torque were measured about the z-axis and converted into coefficients of lift and drag respectively. Wings were positioned upside-down and a cowling was placed over the force sensor to reduce the effect of downwash on the force plate readouts.

Figure S2. Force (mN) traces from spinning mallard wings as analyzed using Chart (v.5.2, ADInstruments, Inc., Colorado Springs, CO, USA). The raw signals have been filtered using a 1-Hz digital low pass filter. Blue = vertical force, lift; red = horizontal force, drag. Grey indicates the region of data measured during the test. Measurements avoided transient forces at start and stop of activity. Because sample intervals $\leq$ 10 seconds, digital filter had no effect upon mean force. A = Day 30, B = Day 60. Scale in A was chosen for improved resolution for this
figure only; torque during motor onset and offset resulted in drag values outside the chosen scale, but data recording was continuous and well within the range of the equipment.

Figure S3. Raw force plate data is displayed from an individual (day 50) mallard. A) All signals for lift were filtered at 1 Hz low pass. The legend shows the active angle of attack for each run. B) All signals for drag were filtered at 1 Hz low pass (legend same as in A). C) Lift data for D50 at 24° $\alpha$ (active), showing unfiltered and filtered (1 Hz low pass) data, and D) drag data for D50 at 24° $\alpha$ (active), showing unfiltered and filtered (1 Hz low pass) data.

Table 1. Gross wing morphology and propeller-spin characteristics for different age classes of mallard (*Anas platyrhynchos*). See Heers et al. (Heers et al. 2011) for comparable measurements in chukar.

Table 2. Feather microstructure during ontogeny in the mallard (*Anas platyrhynchos*). Correlation coefficients ($r$) and probability values ($P$) for peak $C_V:C_H$ as a function of each variable (d.f. = 6 except for data from scanning electron micrographs where d.f. = 2). For comparable data from chukar, see Heers et al. (Heers et al. 2011).

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Figure 5. Ontogenetic trends in mallard feather microstructure. Note number of barbicel hooklets and overlap between barbules. Scale bar 100µm. Images magnified 500X. See Heers et al. (2011) for chukar comparison.
Table 1.

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<tr>
<td></td>
<td>D30</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>637 ± 71</td>
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<tr>
<td>Wing length (cm)</td>
<td>16.9 ± 1.2</td>
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<tr>
<td>Wing chord (cm)</td>
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<td>Aspect ratio</td>
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<td>Area (cm²)</td>
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<td>2nd Moment Area (m⁴)</td>
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<tr>
<td>3rd Moment Area (m⁵)</td>
<td>5.0E-06 ± 1.9E-06</td>
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<tr>
<td>Porosity (%)</td>
<td>17.3±8.7</td>
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<tr>
<td>Camber</td>
<td>0.22 ± 0.06</td>
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<td>Angular velocity (rad s⁻¹)</td>
<td>32.5</td>
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<td>Re</td>
<td>11000 ± 1000</td>
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Table 2.

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<tr>
<td></td>
<td>D45</td>
<td>D50</td>
<td>D55</td>
<td>D60</td>
<td></td>
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<tr>
<td>Feather Unfurling (%)</td>
<td>74±1</td>
<td>73±9</td>
<td>83±3</td>
<td>99±0</td>
<td>0.96 (0.02)</td>
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<tr>
<td>Rachis width (% Adult)</td>
<td>40±4</td>
<td>49±6</td>
<td>64±15</td>
<td>100±0</td>
<td>0.99 (0.01)</td>
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<td>Feather Asymmetry</td>
<td>2.97±0.5</td>
<td>3.89±1.2</td>
<td>4.38±0.1</td>
<td>4.77±0.8</td>
<td>0.92 (0.03)</td>
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<tr>
<td>Barbicels/Barbule</td>
<td>≤1</td>
<td>-</td>
<td>-</td>
<td>1 to 2</td>
<td>0.94 (0.08)</td>
</tr>
<tr>
<td>Barbicel overlap</td>
<td>74±9</td>
<td>-</td>
<td>-</td>
<td>97±12</td>
<td>0.99 (0.03)</td>
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