

RESEARCH ARTICLE

BIOMECHANICS

Morphology, muscle capacity, skill, and maneuvering ability in hummingbirds

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How does agility evolve? This question is challenging because natural movement has many degrees of freedom and can be influenced by multiple traits. We used computer vision to record thousands of translations, rotations, and turns from more than 200 hummingbirds from 25 species, revealing that distinct performance metrics are correlated and that species diverge in their maneuvering style. Our analysis demonstrates that the enhanced maneuverability of larger species is explained by their proportionately greater muscle capacity and lower wing loading. Fast acceleration maneuvers evolve by recruiting changes in muscle capacity, whereas fast rotations and sharp turns evolve by recruiting changes in wing morphology. Both species and individuals use turns that play to their strengths. These results demonstrate how both skill and biomechanical traits shape maneuvering behavior.

A hallmark of powered flight is maneuverability, defined as the ability to actively change speed and/or direction (1). These maneuvers are often used in pursuit, escape, and collision avoidance (2–5). Selection on these behaviors is predicted to recruit a variety of underlying physiological and morphological traits (6, 7). However, understanding how animals achieve high performance is challenging because of the sheer diversity of behaviors and the versatility with which any given maneuver, such as a banked turn, is used (1, 8). Previous experimental studies have used a reductionist approach by constraining animals to complete a predefined task (9–11). Although this can elucidate important biomechanical mechanisms, it cannot capture the degrees of freedom inherent in diverse maneuvering behaviors or the correlations among these behaviors (1, 3–5). Thus, it remains a challenge to link maneuvering performance to its underlying traits (12–15).

We used computer vision to track individual hummingbirds (16, 17), highly agile fliers (4, 18) that can hover and fly backward, and we developed a method to quantify the phenotypic architecture of maneuverability as a multidimensional performance space. The first step is to extract maneuvers that can be classified into three geometric categories (table S1): body translations, body rotations, and complex turns (17). As an example, shown in Fig. 1A is a sequence that begins with a

sharp turn known as a pitch-roll turn (PRT), that occurs when a bird pitches up to decelerate, rolls about the longitudinal axis, and then accelerates again in a new direction. This sequence also includes two translational maneuvers (AccHor, acceleration, and DecHor, deceleration), as well as another complex turn, Arc, which is defined as a smooth arcing turn with no change in vertical position. Using this method to identify a large number of maneuvers from a single species, the Anna's hummingbird (*Calypte anna*), we previously found that solo birds performed similarly to vigorously competing birds in the same environment (17). Furthermore, performance variation within this species in all three types of maneuvers (translations, rotations, and turns) could be explained by individual differences in muscle capacity. By contrast, morphology was only correlated with certain features of turns; narrower wing shapes were associated with the use of Arc turns and high centripetal accelerations. However, *C. anna* has only limited variation in traits known to influence flight efficiency and force production, such as body mass, wing size, and wing shape (19–21). Thus, it was not clear whether these results generalize beyond *C. anna* or whether performance differences at broader taxonomic levels can be understood by using this framework.

In the hummingbird family, there are at least 337 other species with body mass spanning an order of magnitude and wing sizes and shapes that can vary nonisometrically (22–24). Thus, evolution provides an opportunity to examine the independent contributions of size and shape by generating repeated changes in these traits (Fig. 1). The hummingbird family also includes montane taxa that must cope with the additional challenge of flight in low-density air (23, 25). To understand how these factors influence maneu-

verability, we recorded flight maneuvers and morphology from 207 individuals representing 25 neotropical species found at high and low elevation (Fig. 1D). Each bird was recorded alone for 30 min in a large chamber, motivated by the captive environment (supplementary materials, materials and methods, and movie S1). Because we were interested in separating the within- and between-species effects of morphology, we used a different large sample of 263 birds in load-lifting studies to obtain species-average values for body mass, wing size, wing shape, and muscle capacity (supplementary materials, materials and methods, and figs. S1 and S2).

In nature, the ability to outmaneuver competitors, predators, and prey depends on strategic and sensory considerations as well as force production (5, 26–28). A key problem in evolutionary physiology is how to measure meaningful variation in noisy behavioral phenotypes (6, 8). We designed our maneuvering assay to capture a broad range of performance levels from each bird, leveraging the large sample sizes shown in Fig. 1B to recover an accurate signal of individual variation, as defined by moderate to high intertrial repeatability (17). Thus, the analysis does not focus on a single maximal performance value, owing to the constraint of testing performance in a chamber and because it is not possible to unequivocally determine individual variation in maxima for voluntary behaviors.

From the maneuvering trials, we extracted stereotypical maneuvers defined in table S1 that represent the three general categories of translations, rotations, and turns (Fig. 1B). Each maneuver was used by all 25 species. The translational maneuvers included linear accelerations (AccHor) and decelerations (DecHor) limited to the horizontal (*xy*) plane, as well as accelerations that represent monotonic increases in total (*xyz*) velocity (Vel). To calculate performance on these translations, we took the maximum value attained during each maneuver (Fig. 1C) and then found the average for each bird over a 30-min trial. The body rotational maneuvers included sequences when the birds pitched upward (PitchU), pitched downward (PitchD), or made yaw turns (Yaw). We calculated the average rate of body rotation from each maneuver (Fig. 1C), followed by the trial average. For smooth Arc turns, we calculated the turn radius in the *xy* plane (Arc_{radius}), the average velocity in the *xy* plane (Arc_{vel,avg}), and the maximum centripetal acceleration (Arc_{cent,max}). For sharp PRTs, we calculated the magnitude of heading change in degrees (PRT_{degrees}) and the duration in seconds (PRT_{time}). In each case, we calculated a bird's trial average as its performance phenotype. Last, as a measure of the use of different turn strategies, we calculated the percentage of a bird's complex turns that were sharp PRTs (PRT%).

We first asked whether the performance metrics of distinct behaviors are correlated, either negatively, because of trade-offs, or positively, because of general capacities such as muscle size or neural architecture that may influence multiple behaviors (6, 7). We found strong positive correlations,

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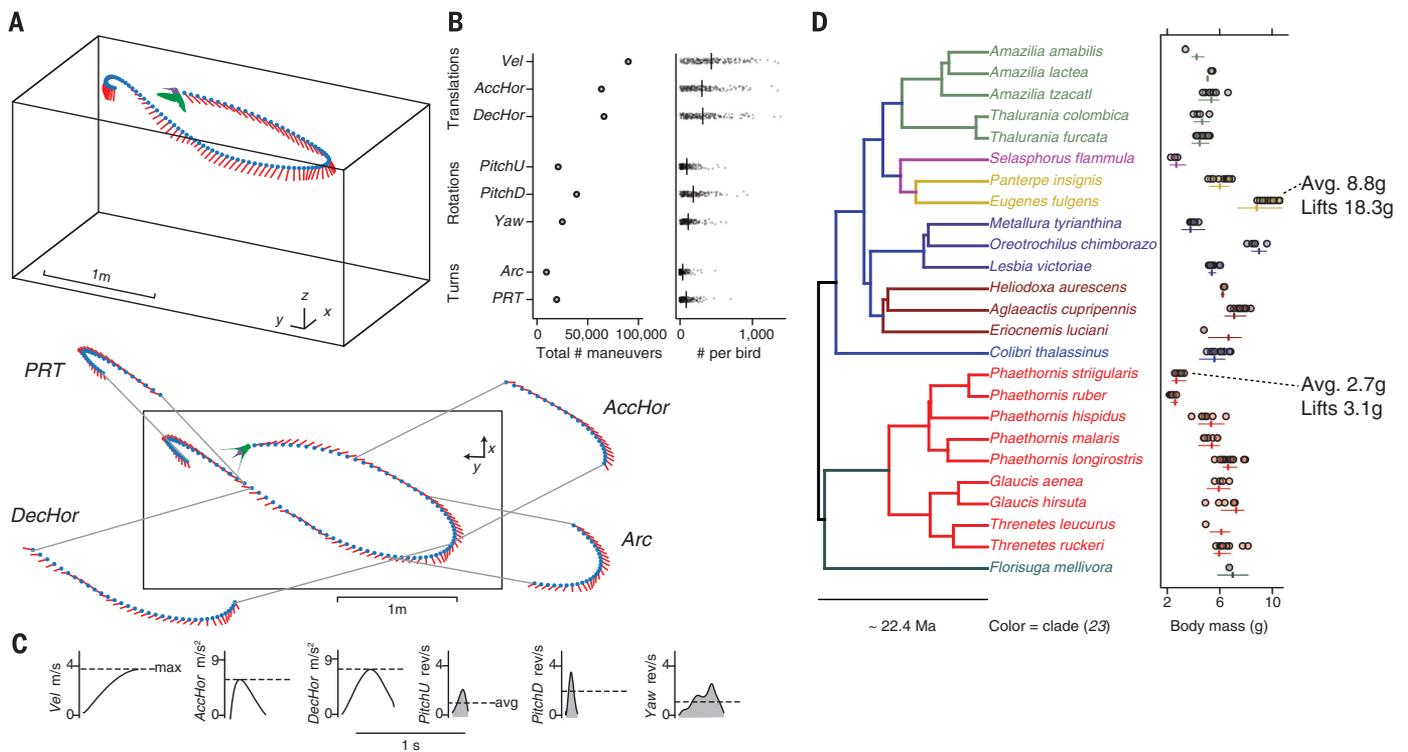


Fig. 1. Flight performance and evolution of Central and South American hummingbirds. (A) A tracking system recorded body position (blue dots) and orientation (red lines) at 200 frames per second. These data were used to identify stereotyped translations, rotations, and complex turns. The sequence in (A) and movie S1 shows a bird performing a pitch-roll turn (PRT) followed by a deceleration (DecHor), an arcing turn (Arc), and an acceleration (AccHor). The sequence duration is 2.5 s, and every 5th frame is shown. (B) The number of translations, rotations, and turns recorded in this study (vertical ticks show the

means). (C) Example translations and rotations illustrating the performance metrics. (D) We obtained performance metrics for 207 individuals from 25 species, ranging in mass from ~2 to 10 g. The phylogenetic tree at left was derived from a recent multilocus analysis (23), with eight principal clades denoted by color. The vertical ticks in (D) show the mean and range for 263 individuals assessed for species average muscle capacity and morphological traits (figs. S1 and S2). The bird in (A) is not drawn to scale. Alternative smoothing of tracking data is provided in figs. S3 and S4 and movie S2.

especially for the rotations and translations (Fig. 2A). This could be caused by coupling owing to constraints of the flight chamber; for example, what accelerates fast may be constrained to decelerate fast in a relatively confined space. If so, we would expect correlations for paired maneuvers within the same bout of flight to be as strong as the corresponding correlations for trial average performance among individuals. Instead, nearly all of the within-flight bout correlations are much weaker than the corresponding correlations among individuals (Fig. 2B and fig. S5). This demonstrates how maneuverability is a suite of correlated behaviors that covary among individuals, similar to other behavioral syndromes (7, 29). Moreover, it shows that our assay of voluntary performance in captivity can reveal the structure of individual behavioral differences.

This also raises the question of whether species differ in these behavioral phenotypes. To test this possibility, we used a discriminant function (DF) analysis to find the combination of behavioral variables that would best distinguish the 25 species. The results indicate that species differ primarily in their performance of complex turns and rotations (Fig. 3A and fig. S6). On the basis of a cross-validation test, we found that birds could be classified to the correct species 34% of the time

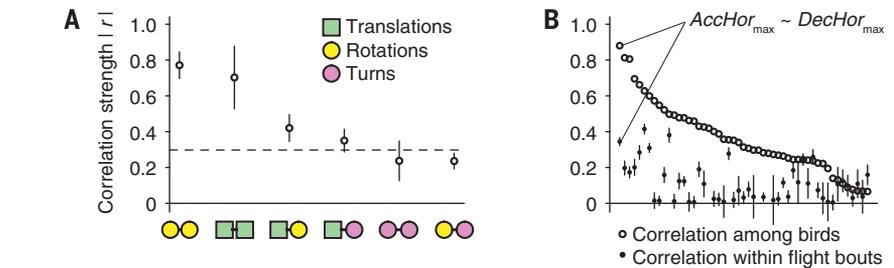


Fig. 2. Performance of different maneuvers is positively correlated. (A) If birds differ in overall maneuverability, we expect trial-average performance to be positively correlated among individuals. Positive correlations are particularly strong for the rotations and translations [means \pm 95% confidence intervals (CIs), $n = 200$ individuals]. The dashed line is the average for all correlations. (B) Positive correlations could be caused by coupling due to constraints of flight in a confined space; if so, it would generate strong within-flight bout correlations. Each column in (B) compares the strength of the average within-flight bout correlation (\pm 95% CI) with the corresponding among-individual correlation. This shows that most of the strong covariance among maneuvers is not due to coupling within bouts of flight. Full analysis is provided in fig. S5.

by using their maneuvers alone, more than expected by chance (Cohen's $\kappa = 0.30$) (Fig. 3A), indicating that differences among species in maneuvering style are subtle but significant. For comparison, the same sample could be classified to the correct species 65% of the time by using morphological traits ($\kappa = 0.61$) (Fig. 3B). An analysis of

phylogenetic structure indicated that on average, closely related species have similar morphologies and maneuvering styles (Fig. 3).

What mechanisms determine these evolved differences? Given that many maneuvers involve reorienting the body (10, 15, 27, 30), we asked whether performance changes with body mass

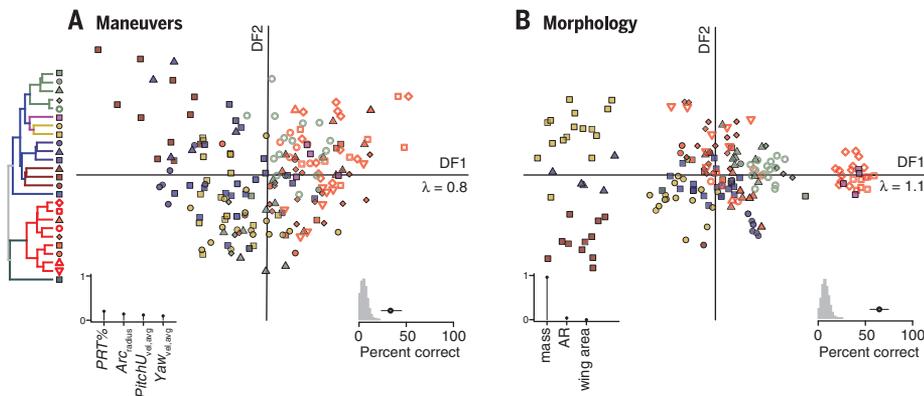


Fig. 3. Species differ in maneuvers and morphology. (A to B) We used discriminant functions (DFs) to classify 25 species based on (A) maneuvering and (B) morphological phenotypes ($n = 180$ birds). Each species is represented by a different color-symbol combination. The x axis (DF1; arbitrary units) accounts for most of the variation in the data space [33% in (A); 85% in (B)]. In both (A) and (B), DF1 has a Pagel's λ significantly greater than 0, indicating that closely related species resemble each other more than species drawn at random (all $P < 0.03$). (Left insets) The top DF1 loadings, demonstrating that species mainly differ in (A) their performance of complex turns and rotations and (B) body mass. (Right insets) The results of cross-validation, as the median percent of test data that was classified to the correct species ($\pm 95\%$ central range). In both (A) and (B), classification accuracy was significantly better than expected (inset histograms = 10,000 randomized permutations). However, morphological classification was nearly twice as accurate, demonstrating that the species differ more in morphology than maneuvering style. Additional loadings are available in fig. S6.

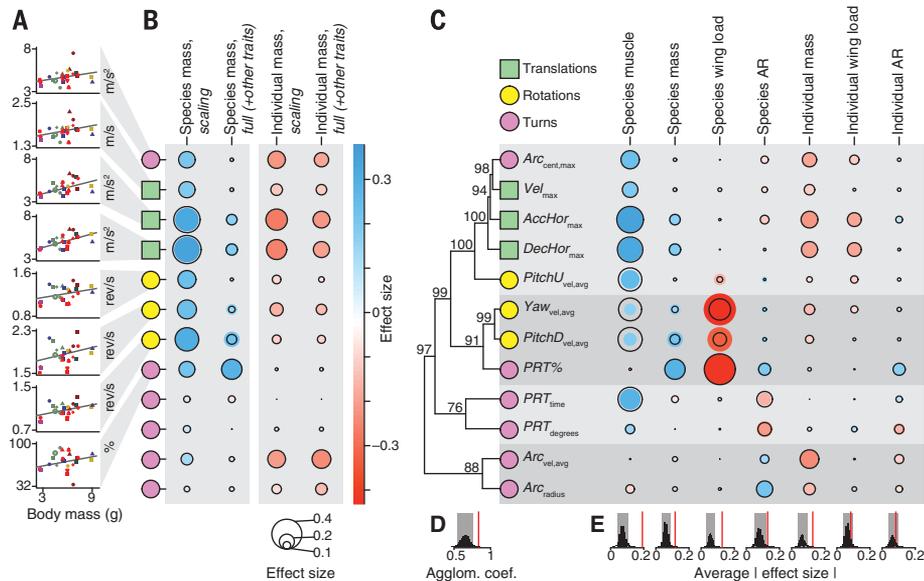


Fig. 4. Different flight maneuvers are determined by different biomechanical traits. (A) Species mass is positively associated with several maneuvers. (B) Effect sizes from scaling models (mass only) and full models (mass + other traits). Each row is a maneuver, ordered to match (C). Effect sizes are standardized to be comparable across traits (columns) and maneuvers (rows). The positive effects of species mass (blue) are attenuated when the other traits are added in the full model, except for PRT%. The negative effects of individual mass (red) are consistent. (C) Results of the full models show how maneuvers are clustered according to their associations with different biomechanical traits. AR stands for wing aspect ratio, a measure of wing shape. The bootstrap support (percent) is shown for each node in the dendrogram. (D) The agglomerative coefficient measures the strength of clustering and is significantly greater than that of randomized data (black histogram; shading shows the 95% central range for 10,000 permutations). (E) The mean effect magnitude for each trait, averaged across all maneuvers. The outlined circles in (B) and (C) show the results of analyses that account for phylogenetic relationships ($n = 187$ birds, except 180 for Arc). Full analysis is provided in figs. S7 to S9.

(1, 8). Using a recent multilocus phylogeny for cross-species comparisons (23), we modeled each performance metric, entering species-average body mass and individual mass (relative to conspecifics) as predictors. Analyzing both levels of biological variation is necessary to test whether the “within-species” effects of a trait are broadly consistent. Moreover, it also tests whether the “between-species” and within-species effects of a trait diverge, as a result of other compensatory traits (8, 31). This analysis also accounted for the elevation where the species reside and were tested. We found that hummingbird species with greater body mass perform faster translations, centripetal accelerations, and rotations (Fig. 4A and movie S1). However, within a species, heavier individuals tend to perform slower translations and centripetal accelerations (Fig. 4B).

To determine the reason for this scaling result, we reran the analysis above but added muscle capacity and wing morphological traits as additional predictors (Fig. 4C). These “full models” revealed that enhanced translational and centripetal accelerations can be attributed to greater species muscle capacity rather than body mass per se, whereas enhanced rotational speeds can be attributed to a combination of greater muscle capacity and lower wing loading (Fig. 4C). This result explains why hummingbird maneuverability scales positively with species mass, even though mass has the opposite effect on individual performance: Larger species can achieve maneuverability through the evolution of disproportionate increases in muscle capacity and wing size (24). One exception is PRT%, the only metric showing a strong relationship with species mass independent of the other traits, to which we will return later.

The distinct trait effects shown in Fig. 4C suggested that different maneuvers rely on different biomechanical traits. To quantitatively test this hypothesis, we used hierarchical clustering to group the performance metrics according to trait effect sizes and found strong support for four terminal groups (Fig. 4D). The first cluster includes all three translational maneuvers, the centripetal accelerations, and the upward rotations; these maneuvers largely depend on the effect of species muscle capacity. A second cluster includes the downward and yaw rotations and the relative use of turns, which largely depend on species wing loading. The third and fourth clusters include the size and speed of turns, which are the features most strongly associated with species aspect ratio (AR), a measure of wing shape. Thus, species-level evolutionary changes in muscle capacity and wing morphology affect different, correlated suites of behaviors.

Our analysis identifies burst muscle or the engine capacity of a species as having the strongest overall effect on multiple maneuvers (Fig. 4E). This extends our previous result that muscle capacity variation determines individual performance within a species (17). We measured load-lifting and maneuvering using different individuals, which provides a strong test of the hypothesis that evolved changes in muscle capacity influence

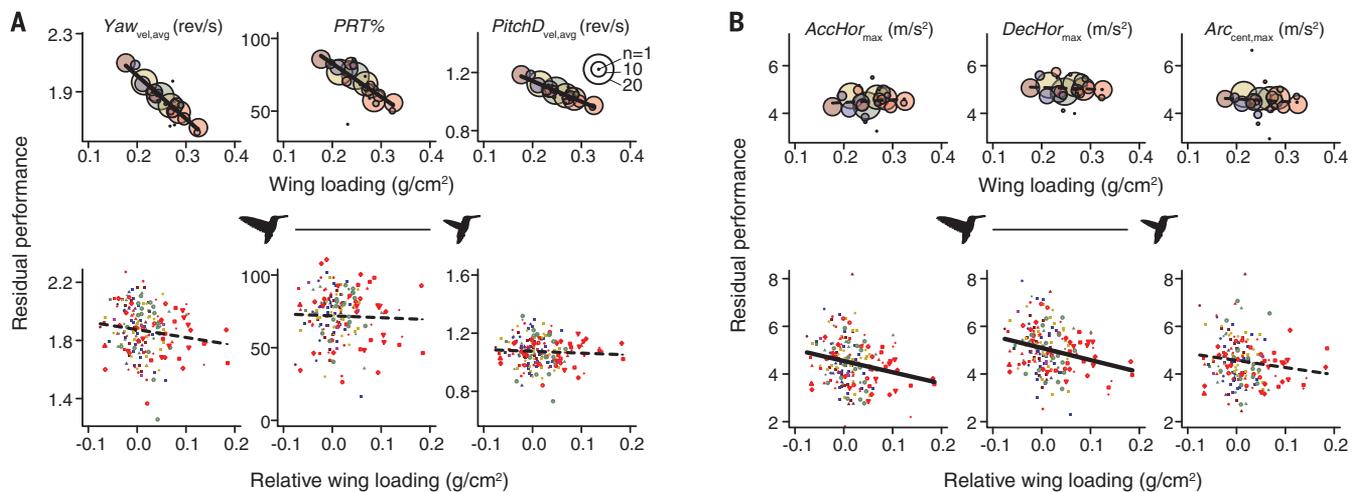


Fig. 5. Species and individual wing size affect different maneuvers.

Partial effect plots illustrate the relative effect of wing loading given the other effects in the statistical model. Dotted lines indicate nonsignificant effects. **(A)** Yaw rotations, the use of complex turns, and downward rotations are strongly dependent on species wing loading (top row). However, these same maneuvers are not significantly associated with an

individual's wing loading relative to conspecifics (bottom row).

(B) Horizontal acceleration, deceleration, and centripetal acceleration are not associated with species wing loading (top row); however, these are the metrics that are most strongly associated with individual wing loading (bottom row). Colors indicate clade, as in Fig. 1. Bubble diameters represent the sample sizes for the 25 species.

performance. Muscle capacity differences among and within species are likely both due to variation in muscle size (32–34) because, as the evidence to date indicates, small birds have flight muscles composed exclusively of fast oxidative glycolytic fibers (35).

It is thought that the flight performance envelope is also determined by wing size (36). Specifically, a larger wing area relative to body mass (lower wing loading) is predicted to enhance acceleration and turning performance (37, 38). We found that evolved interspecific differences in hummingbird wing loading are strongly associated with two of the rotational maneuvers and the use of sharp, pitch-roll turns (Fig. 5A). Therefore, sharp turns and fast rotations—the same behaviors that best differentiate species (fig. S6)—are associated with disproportionate increases in wing size (24). We also found that individuals with higher wing loading relative to their conspecifics tend to perform slower accelerations (Fig. 5B). Given that muscle capacity is the primary species-level trait associated with accelerations (Fig. 4C), this result suggests that evolved changes in muscle capacity can compensate for relatively small wings. A corollary is that smaller wings are not always detrimental because they may have efficiency advantages, depending on the environment and mode of flight.

Our results also illustrate why the effects of individual wing size and body mass were not detected in a previous study of just one species (17): They are too weak to detect in small samples (Fig. 5B and fig. S10), highlighting the need for large sample sizes. With respect to individual body mass, birds often experience fluctuations of 10 to 20% within hours (39, 40). Our analysis predicts that these body mass fluctuations will affect translational and centripetal accelerations in many species.

Although wing shape determines efficiency (41), it has relatively weak effects on maneuverability, with the only significant result being a positive association between individual aspect ratio (AR) and the use of sharp pitch-roll turns, PRT% (Fig. 4C). The direction of this result is surprising because we previously found that AR was negatively associated with PRT% within one species (*C. anna*) (17). Further analysis here explains why: AR has either a negative, neutral, or positive association with PRT%, depending on the species (fig. S11). In hummingbirds, an individual's AR often changes dramatically as a result of damage to the wings and molt, and these changes can even exceed the variation among species (42). Many individuals in this study had wings that were naturally damaged or molting, capturing a wide range of AR values (fig. S1). Our results therefore raise the possibility that maneuvering flight is either robust to these transitory changes in wing shape, or it may be affected in different ways, depending on the species, its morphology, and its use of different behaviors. These hypotheses could be tested through a combination of natural and experimental alterations of wing phenotypes.

The only aspect of maneuvering that differed among elevations, independent of other traits, was the use of complex turns; species captured and tested at high elevation used proportionately fewer sharp PRTs and more smooth Arcs (Fig. 6A). This is consistent with a previous result that low-elevation birds reduce their use of PRTs when moved to high elevation (25), and so it suggests a shared constraint. Complex turns are also associated with morphological evolution; heavier species and those with lower wing disk loading use proportionately more sharp turns and fewer smooth Arcs (Fig. 6B). This could be due to biomechanical differences that influence the ef-

iciency of Arc and PRT maneuvers (such as wingbeat frequency, inertia, and/or mass distribution). Another hypothesis is suggested by the fact that individuals use more Arcs in the presence of another bird (17). Smaller species and those with higher wing loading may use arcing turns more often for a tactical or safety advantage. These hypotheses could be tested by manipulating mass and wing phenotypes during competition among different species (13).

How does the use of a behavior relate to its performance? We define maneuvering fatigue as any process that causes the individuals that use a particular maneuver more often to perform it at a lower level. Conversely, maneuvering skill is any process that causes the individuals that use a maneuver more often to perform it at a higher level. Our results show that performance and frequency of use are often related and that skill predominates. All else being equal, birds that perform more pitch-downward and -upward rotations, and more total velocity increases, perform these respective maneuvers more rapidly; birds that perform more sharp PRT turns also do so for larger heading changes in less time (fig. S12). We used further analysis of PRT% to test the use of complex turns at both the species and individual level. Species that use proportionately more Arcs tend to perform their Arcs with greater centripetal acceleration (Fig. 6B); they are able to redirect more turning force laterally while maintaining altitude. This trend is also recapitulated within species (Fig. 6C). Thus, the complex turns demonstrate that both species and individuals play to their strengths. How do these preferences for particular maneuvers arise? Are they driven by physiological and/or ecological differences, or do they represent random or neutral variation? These questions could be addressed by examining species differences in sensory systems

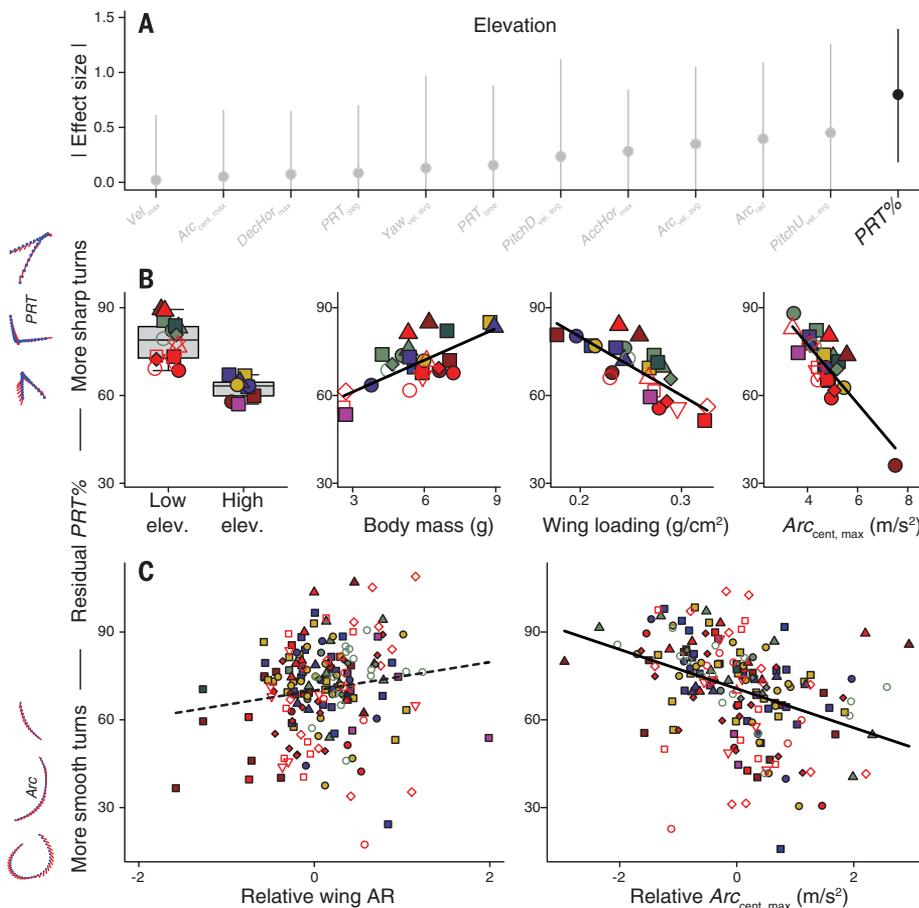


Fig. 6. Complex turns are associated with the environment, morphology, and skill. (A) The use of sharp versus smooth turns, PRT%, was the only behavior that differed among high- and low-elevation species. Effect sizes account for phylogenetic relationships ($\pm 95\%$ highest posterior density intervals). (B and C) Partial effect plots illustrate the relative effect of each variable on PRT%, given the other effects in the statistical model ($n = 180$ individuals). (B) All else being equal, low-elevation species, larger-mass species, and those with lower wing loading use proportionately more sharp PRTs (and fewer Arcs). (C) Individuals with longer wings (high AR) use more sharp turns, although further analysis shows how this association can vary, depending on the species (fig. S11). Species and individuals that perform Arcs with greater centripetal acceleration also use proportionately more Arcs [(B) and (C), rightmost column], indicating that skill predominates over fatigue in the use of these complex turn maneuvers. Results are robust to removing the high-leverage species with $n = 1$ individual in (B).

and the development of locomotor ability, as well as functional ecology.

A key result of our comparative analysis is that evolved changes in the wings primarily determine turns and rotations, whereas evolved changes in muscle capacity primarily determine translations. This indicates that different flight maneuvers evolve by recruiting different traits. Our method provides a framework to now investigate the underlying genetic changes and adaptive fitness landscapes that have shaped the evolution of maneuvering flight. For birds, the relevant ecological factors may include predation, competition, and socially selected displays as well as elevational habitat (1, 18, 25, 33). An important next step is to determine how translations, rotations, and turns are used in other behavioral contexts and how suites of maneuvering behaviors are used by other flying animals.

Such comparisons may reveal performance trade-offs that favor different maneuvering and morphological phenotypes (6). Moreover, the framework we provide can be used to test these ideas in more complex environments, once sufficiently small biologging tools become available. Although we have focused here on maneuvers that are shared among species, going forward it will be important to consider how these behaviors are combined into higher-order sequences and how novel maneuvers and sequences evolve.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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Movies S1 and S2

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Making quick turns

Hummingbirds are well known for their impressive maneuvering during flight. Dakin *et al.* used a computer vision approach to characterize the details of flight in >200 hummingbirds from 25 species (see the Perspective by Wainwright). Larger species had enhanced agility owing to increased muscle mass. In all species, muscles dictated transitional movement, whereas wing shape facilitated sharp turns and rapid rotations. Species, and individuals within species, played on their strengths by combining inherent traits and learned skills.

Science, this issue p. 653; see also p. 636

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