# MORPHOLOGICAL ASPECTS OF AVIAN TAIL MOVEMENTS: A FUNCTIONAL APPROACH IN HIRUNDINES

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ABSTRACT.—It has been proposed that the aerodynamically optimal tail shape in birds should be triangular when spread and forked when closed. According to this aerodynamic model, any area distal to the point of maximum width contributes drag, which is proportional to total tail area, but not lift. One assumption of this model seems to be uniformity in structures responsible for tail movements (i.e. tail muscles) among species. We tested for different muscular arrangements in species with different tail shapes. By dissecting tail muscles in three hirundine species (Barn Swallow [*Hirundo rustica*], Common House-Martin [*Delichon urbica*], and Bank Swallow [*Riparia riparia*]), we demonstrate anatomical differences associated with deeply forked tails and speculate that such differences compensate for the increased cost of longer feathers. Therefore, we propose that reliable assessment of the aerodynamic cost of tails should be based on tail shape as well as internal anatomical structures such as muscles. *Received 13 September 1995, accepted 28 November 1995.*

AMONG PASSERINE SPECIES, members of the family Hirundinidae spend the greatest proportion of their time flying. Their survival depends in large part upon agility and maneuverability. Being species that rely heavily on flight for foraging, wing and tail shapes are of great aerodynamic importance, as they represent the most important lifting surfaces (Norberg 1990, Thomas 1993). Recently, it has been proposed by applying lifting-surface theory that any area in the tail distal to the point of maximum continuous width adds drag, but not lift (Thomas 1993). However, Norberg (1994) has demonstrated experimentally that tail streamers improve tail aerodynamic efficiency and enhance flight performance by increasing lift and reducing the turning radius.

Balmford et al. (1993) examined the aerodynamic implications of tail elongation by modelling progressive elaboration from short, simple tails to long, deeply forked tails. Their model suggests that aerodynamic costs increase as tails become more deeply forked. According to this model, Barn Swallows (*Hirundo rustica*) with sexually size-dimorphic, deeply forked tails suffer aerodynamic costs of tail elongation relative

to Common House-Martins (*Delichon urbica*) and Bank Swallows (*Riparia riparia*), which have shallowly forked tails that are sexually monomorphic. The slender lifting-surface model shows that at a given angle of attack, the forces generated by the tail depend on only two features of morphology, viz. tail width and tail area, both of which depend on tail shape and how widely the tail is spread (Thomas 1993). Considering variables included in the model, it appears that the authors have not considered that other variables concerning tail morphology could affect the model. That is, it seems that the model assumes that internal structures responsible for tail movements (i.e. tail muscles) are uniform.

Although it generally has been assumed that muscular morphology is rather uniform within avian families (Gadow 1893, Berger 1969), several studies have demonstrated important differences between closely related species (e.g. McKitrick 1986, Moreno and Carrascal 1993). Such differences have functional explanations regarding the way in which species behave. As a group, hirundines are assumed to be morphologically uniform (Sheldon and Winkler 1993) because their shared body plan has been shaped by aerial insectivory. In spite of this apparent uniformity, some species differ in hindlimb musculature (e.g. reduction in size and/ or absence of some leg muscles; Gaunt 1969,

Moreno and Carrascal 1993). Here, we provide a detailed description of the tail musculature of three swallows (Barn Swallow, Common House-Martin, and Bank Swallow). We document a relationship between tail musculature and tail shape, and test the possibility that a larger muscular support will compensate for the increased cost of longer feathers. Considering that tail-depressor muscles are the main structures responsible for counteracting the upward action of air flow during flight, we predict that species having longer tails will have depressor muscles that are modified to develop more force upon contraction. An increase in the force developed by tail depressors might have two advantages from a functional point of view. First, to compensate for the possible aerodynamic costs associated with a deeply forked tail (Balmford et al. 1993), and second, to compensate for the increased load associated with heavier feathers (because feathers represent part of the load that muscles must move upon contraction).

## MATERIALS AND METHODS

The tail muscles of fluid-preserved adults were studied by dissection: Barn Swallow ($n = 16$; Museo Nacional de Ciencias Naturales of Madrid, specimen numbers MNCN 21678 to 21693), Common House-Martin ($n = 8$; MNCN 21704 to 21711), and Bank Swallow ($n = 6$; MNCN 21698 to 21703). Right and left sides were dissected in all specimens (Raikow et al. 1990). Both sexes were equally represented in our samples except for the Bank Swallow, for which two males and four females were available for dissection. Only the main muscles accounting for the most important movements of the tail (elevation, depression, and spreading; Raikow 1985) were dissected: M. levator caudae, M. lateralis caudae, M. pubocaudalis externus, M. pubocaudalis internus, and M. depressor caudae. Actions of the muscles were taken from the literature (Fisher 1946, 1957; Owre 1967; Raikow 1970, 1985). Anatomical nomenclature follows Baumel et al. (1993).

The gross morphology of the muscles was studied using a Wild M5A stereo dissecting microscope at magnifications of 5 to 20×, aided by an iodine muscle stain to enhance visibility of the muscle tissue (Bock and Shear 1972). After muscles were removed, their length (from origin to insertion) and dry mass were recorded (Table 1). Because most of the muscles were parallel or slightly unipennate, we assumed that the force developed upon contraction is directly related to their mass (Bock 1974). However, muscle (M.) levator caudae is deeply bipennate. In this case, we also measured fiber length and pennation angle (i.e. angle

between the muscle fiber and the line of action of the whole muscle). We calculated the force ($F$) developed by this muscle (in N) by the following equation (Table 1):

$$F = k\{[m \cdot \sin (2\alpha)/2 \cdot \rho \cdot l \cdot \sin \alpha] \cos \alpha\}, \qquad (1)$$

where $k$ is a constant for the unit of force development ($N \cdot m^{-2}$; Bock 1974), $m$ is the muscle's dry mass (kg), $\rho$ is the muscle's density (assumed to be $1,060 \text{ kg} \cdot m^{-3}$; Bennett 1995), $l$ is the muscle's mean fiber length (m), and $\alpha$ is the mean pennation angle in degrees (Bock 1974, Biewener 1992).

Length and mass of the first, second, and central rectrices (left and right sides) were also determined after being removed from the specimens (Table 1). We did not record tail skeletal length because it would have been difficult to measure accurately in fluid-preserved specimens. All linear measurements and pennation angles were determined with the aid of a Genitizer GT 1212B-Plus digitizer tablet (Full-Featured CAD Software Cas-CAD II), the former being recorded to the nearest 0.01 mm. Feather and muscle masses were recorded with a precision balance (± 0.0001 g). For all paired biometrical variables, we used the mean of the left and right values per bird in the analyses.

To correct for differences in size among species, we obtained size-corrected measurements as the standardized residuals of the linear regression of each biometrical variable on the keel length (Table 2), measured from the apex carinae to the central point of the metasternum. Considering that the goal of these analyses was to control for the effects of size, we used Model I regression because it is the only technique producing residuals exactly uncorrelated with the independent variable (Harvey and Pagel 1991). We tested for differences among species and sexes and their interaction for the morphometric variables using two-way ANOVAs, and we adjusted $P$ values using the Bonferroni adjustment (Maxwell and Delaney 1989). We used Tukey multiple range tests for unequal sample sizes to compare mean values. Drawings were made with the aid of a camera-lucida microscope attachment.

## RESULTS

### MUSCULAR DESCRIPTION

A detailed description of each muscle as it appears in the Barn Swallow is given. If no comments are made, the morphology in Common House-Martins and Bank Swallows is similar to that of Barn Swallows. No morphological (qualitative) differences were found between left and right sides in any species.

*M. levator caudae.*—The most superficial muscle of the tail arises fleshy from the caudal third

TABLE 1.  Biometrical variables ($\bar{x} \pm$ SD) from specimens of Barn Swallow ($n = 16$), Common House-Martin ($n = 8$), and Bank Swallow ($n = 6$). Lengths in mm, masses in mg, pennation angle in degrees, and force in N.

| | Barn Swallow | | Bank Swallow | | Common House-Martin | |
|---|---|---|---|---|---|---|
| | $\bar{x}$ | SD | $\bar{x}$ | SD | $\bar{x}$ | SD |
| First rectrix length | 103.61 | 8.764 | 59.08 | 2.382 | 59.43 | 4.959 |
| First rectrix mass | 15.2 | 1.25 | 8.4 | 0.56 | 10.2 | 1.01 |
| Second rectrix length | 68.95 | 2.022 | 58.05 | 1.929 | 59.15 | 1.914 |
| Second rectrix mass | 10.6 | 0.60 | 7.2 | 0.52 | 8.3 | 0.70 |
| Central rectrix length | 48.75 | 1.838 | 47.83 | 2.138 | 44.87 | 1.678 |
| Central rectrix mass | 6.2 | 0.52 | 4.8 | 0.56 | 4.9 | 0.24 |
| M. levator caudae (length) | 14.60 | 1.094 | 13.48 | 0.402 | 15.42 | 0.904 |
| M. levator caudae (fiber length) | 5.86 | 0.484 | 4.96 | 0.295 | 5.68 | 0.684 |
| M. levator caudae (pennation angle) | 32.83 | 3.841 | 33.27 | 1.922 | 31.15 | 2.731 |
| M. levator caudae (force) | 0.0014 | 0.0002 | 0.0013 | 0.0001 | 0.0017 | 0.0004 |
| M. lateralis caudae (mass) | 1.2 | 0.36 | 0.9 | 0.15 | 1.5 | 0.34 |
| M. lateralis caudae (length) | 7.92 | 0.688 | 6.99 | 0.274 | 8.21 | 0.563 |
| M. pubocaud. ext. (mass) | 2.6 | 0.55 | 2.4 | 0.16 | 2.9 | 0.38 |
| M. pubocaud. ext. (length) | 9.12 | 0.924 | 7.56 | 1.039 | 10.50 | 1.170 |
| M. pubocaud. int. (mass) | 3.1 | 0.58 | 2.2 | 0.53 | 3.0 | 0.67 |
| M. pubocaud. int. (length) | 9.96 | 0.902 | 8.86 | 0.615 | 11.29 | 1.420 |
| M. depressor caud. (mass) | 8.3 | 2.26 | 6.4 | 1.1 | 7.5 | 1.29 |
| M. depressor caud. (length) | 11.61 | 0.848 | 9.82 | 0.519 | 12.01 | 0.732 |
| Keel length | 20.78 | 0.841 | 18.51 | 0.354 | 19.56 | 1.322 |

of the dorsal iliac plate (Fig. 1). The right and left sides of the muscle converge bipennately on the midline. It gives rise to multiple slips, which insert on the dorsalis process of the last four free caudal vertebrae and on the pygostyle. The posterior portion fans out to insert into the fascial covering of the bases of the four central rectrices. The main action of this muscle is to elevate the entire tail.

*M. lateralis caudae.*—Its origin is by fleshy fibers from the transverse processes of the second and third free caudal vertebrae, covered by the levator caudae. Fibers run posterolaterally in an almost parallel arrangement, but the belly becomes spindle-shaped at its caudal end (Fig. 1). The insertion is by tendinous and fleshy fibers on the base of the outermost rectrix dorsolaterally. Contraction of this muscle results in spreading of the tail, because the rectrices are interconnected on each side by a webbing of connective tissue. It also elevates lightly the outermost rectrix.

TABLE 2.  Linear regressions of biometrical variables ($y$) on keel length ($x$). Degrees of freedom 1 and 28 in all cases ($n = 30$). Lengths in mm, masses in g, and force in N.

| Variable ($y$) | $R^2$ | $P$ | Equation |
|---|---|---|---|
| First rectrix length | 0.43 | <0.001 | $y = -157.9 + 12.04x$ |
| First rectrix mass | 0.44 | <0.001 | $y = -0.02 + 0.00164x$ |
| Second rectrix length | 0.41 | <0.001 | $y = 8.74 + 2.77x$ |
| Second rectrix mass | 0.38 | <0.001 | $y = -0.006 + 0.00076x$ |
| Central rectrix length | 0.18 | 0.021 | $y = 31.47 + 0.80x$ |
| Central rectrix mass | 0.35 | <0.001 | $y = -0.00197 + 0.00038x$ |
| M. levator caudae (length) | 0.01 | 0.614 | $y = 12.91 + 0.084x$ |
| M. levator caudae (force) | 0.00 | 0.921 | $y = 0.00136 + 0.0000042x$ |
| M. lateralis caudae (length) | 0.06 | 0.209 | $y = 5.15 + 0.1330x$ |
| M. lateralis caudae (mass) | 0.17 | 0.024 | $y = -0.0011 + 0.00012x$ |
| M. pubocaud. ext. (length) | 0.02 | 0.407 | $y = 5.729 + 0.172x$ |
| M. pubocaud. ext. (mass) | 0.12 | 0.056 | $y = 0.000021 + 0.000132x$ |
| M. pubocaud. int. (length) | 0.00 | 0.852 | $y = 10.814 - 0.036x$ |
| M. pubocaud. int. (mass) | 0.25 | 0.005 | $y = -0.0023 + 0.00026x$ |
| M. depressor caud. (length) | 0.13 | 0.052 | $y = 5.284 + 0.303x$ |
| M. depressor caud. (mass) | 0.14 | 0.038 | $y = -0.0039 + 0.00058x$ |

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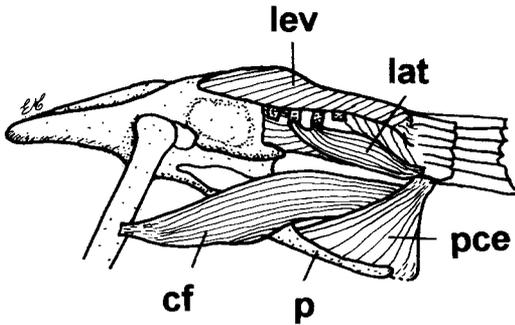


Fig. 1. Lateral view of superficial muscles of tail of Barn Swallow. Abbreviations: (cf) muscle caudoiliofemoralis, pars caudofemoralis; (lev) muscle levator caudae; (lat) muscle lateralis caudae; (p) pubis bar; and (pce) muscle pubocaudalis externus.



Fig. 2. Lateral view of tail of Common House-Martin after removing muscle lateralis caudae and muscle pubocaudalis externus. In Barn Swallows, muscle pubocaudalis internus is as in Common House-Martin, but lacking tendinous raphe. Abbreviations: (cf) muscle caudoiliofemoralis, pars caudofemoralis; (dep) muscle depressor caudae; (lev) muscle levator caudae; (p) pubis bar; (pci) muscle pubocaudalis internus; and (r) raphe.

*M. pubocaudalis externus.* —This triangular muscle originates fleshy from the caudal half of the pubis. Caudally, the origin becomes aponeurotic from the membrane covering the vent. Fibers run caudodorsally to insert by fleshy and tendinous fibers on the base of the outermost rectrix lateroventrally (Fig. 1). When left and right muscles are contracted, the entire tail is depressed, but acting unilaterally it rotates the tail along its longitudinal axis.

*M. pubocaudalis internus.*—This muscle underlies M. pubocaudalis externus. It arises fleshy from the pubis bar and aponeurotic from the membrane covering the vent. Fibers in a lightly unipennate arrangement insert by fleshy and tendinous fibers on the pygostyle ventrolaterally. In Common House-Martins and Bank Swallows, the belly is divided by a tendinous raphe from which two tendons originate (Fig. 2). Cranially, a tendon arises to insert on the belly of the M. caudoiliofemoralis, pars caudofemoralis. From the raphe caudally a second tendon originates to insert onto the septum supracloacale, in a lateral position relative to the cloaca. As M. pubocaudalis externus, this muscle depresses the tail if both the left and right muscles contract at once, but it can also rotate the tail if both muscles act unilaterally.

*M. depressor caudae.*—It is the deepest muscle that lies on the ventral surface of the free caudal vertebrae and the pygostyle. The muscle arises fleshy from the caudal border of the ilium and from the ventral surface of the transverse process of the last fused vertebra of the synsacrum (Fig. 2). Some fleshy fibers also originate ventrally from the outermost extreme of the transverse processes of the free caudal vertebrae. Fibers run posteromedially to insert on the ventral surface of the hemal spines and vertebral centrum of the free caudals, and, laterally in the ventral pygostyle. Although superficially fibers run in a parallel arrangement, deeper fibers present a unipennate arrangement from the transverse process to the centra of the next free caudal vertebrae. It depresses the tail, if bilateral activity of the muscles is involved, but possibly aids tail rotation if the muscles act unilaterally.

MORPHOMETRY

Differences in both external (feathers) and internal (muscles) variables were apparent among species (Table 3). Feather lengths (Fig. 3A, B) and the mass of the first and the second rectrices differed significantly among species. However, in muscles only the length of the M. pubocaudalis externus (Fig. 3C), M. pubocaudalis internus, and M. depressor caudae differed (Fig. 3D) among species. No significant differences were found between sexes, and the interactions between sex and species also were nonsignificant for all variables (Table 3).

DISCUSSION

Our study of tail structure in hirundines has shown that rectrix dimensions, as well as the

TABLE 3. Biometrical differences between species, sexes, and their interaction for external (feathers) and internal (muscles) variables. Values are $F$-values from two-way ANOVAs. After Bonferroni adjustment, $F = 7.42$ at $P = 0.05$; $F = 10.27$ at $P = 0.01$. Degrees of freedom 2 and 24 for species, 1 and 24 for sex, and 2 and 24 for their interaction. Significant differences between pairs of species shown in last column (Tukey test; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Abbreviations: (Du) *Delichon urbica*; (Hr) *Hirundo rustica*; (Rr) *Riparia riparia*; and (M) muscle.

| Variable | Species | Sex | Interaction | Difference between sexes |
|---|---|---|---|---|
| First rectrix length | 18.642** | 1.191 | 2.254 | Hr > Rr*, Hr > Du*** |
| First rectrix mass | 9.663* | 1.019 | 0.934 | Hr > Rr*, Hr > Du** |
| Second rectrix length | 11.477** | 2.238 | 0.016 | Hr > Du** |
| Second rectrix mass | 7.566* | 1.328 | 0.026 | Hr > Rr*, Hr > Du* |
| Central rectrix length | 9.490* | 0.002 | 0.296 | Hr > Du*, Rr > Du** |
| Central rectrix mass | 5.477 | 0.073 | 0.669 | |
| M. levator caudae (length) | 5.789 | 0.318 | 1.053 | |
| M. levator caudae (force) | 6.440 | 4.259 | 3.412 | |
| M. lateralis caudae (length) | 4.607 | 0.387 | 0.301 | |
| M. lateralis caudae (mass) | 4.227 | 0.069 | 0.863 | |
| M. pubocaud. ext. (length) | 14.159** | 2.277 | 1.676 | Hr < Du**, Rr < Du*** |
| M. pubocaud. ext. (mass) | 3.118 | 0.078 | 3.323 | |
| M. pubocaud. int. (length) | 9.996* | 2.298 | 1.646 | Hr < Du*, Rr < Du*** |
| M. pubocaud. int. (mass) | 1.162 | 3.736 | 2.254 | |
| M. depressor caudae (length) | 9.417* | 2.335 | 0.792 | Hr > Rr*, Rr < Du*** |
| M. depressor caudae (mass) | 0.399 | 0.133 | 1.437 | |
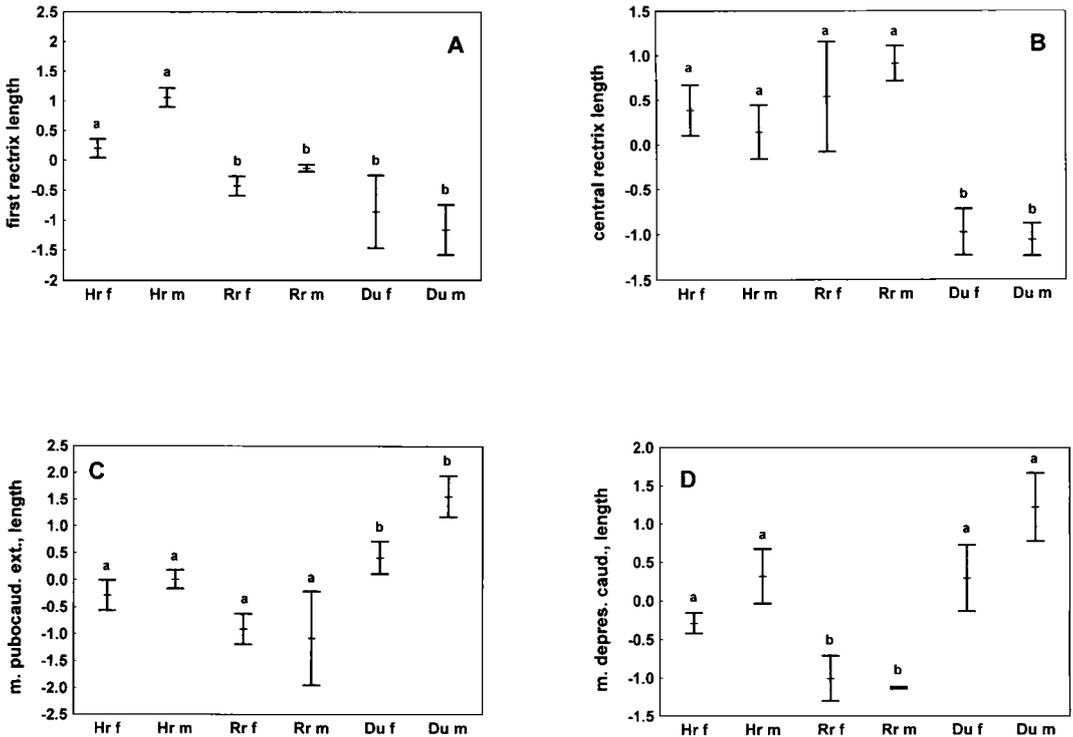


Fig. 3. Differences among species and between sexes in lengths (mm) (A) of the first rectrix (using residuals on keel length), (B) central rectrix, (C) muscle pubocaudalis externus, and (D) depressor caudae. Vertical bars denote ± SE. Similar lowercase letters near bars denote homogeneous groups not statistically different at $P < 0.05$ (Tukey test). Abbreviations: (Hr f) *Hirundo rustica* female; (Hr m) *H. rustica* male; (Rr) *Riparia riparia*; and (Du) *Delichon urbica*.

dimensions of some tail muscles, differ among species. The tail and the wings represent the most important lifting surfaces. Tail shape, but also morphological structures responsible for tail movements, should be of enormous importance in maximizing aerodynamic lift and reducing drag. As for any lifting surface, the tail must counteract the upward action of air flow (i.e. aerodynamic load). This counteractive effect is accomplished by tail-depressor muscles. To maintain a given angle of attack might be less costly for species having stronger depressor muscles. Therefore, the lift-to-drag ratio might be affected by the morphology of these depressor muscles. Moreover, aerodynamic loads are not the only ones against which depressor muscles must work. Feather mass and overall tail length (which determines the lever arm of the system) are additional loads that depressor muscles must move upon contraction. We documented significant differences among species in both feather dimensions and some tail-depressor muscles. Considering changes in functional properties related to morphological modifications, we tested the hypothesis that a larger muscular support will compensate for the increased cost of bearing a long, forked tail.

With respect to feather variables, the Barn Swallow is clearly separated from the other two species by having both the longest and heaviest outermost (first and second) tail feathers (Table 3, Fig. 3A). However, the relative length of the central rectrix in the Barn Swallow is as long as that in the Bank Swallow and significantly longer than that in the Common House-Martin (Fig. 3B). The mass of the latter feather is lowest in the Common House-Martin, although a significant difference occurs only between the Common House-Martin and the Barn Swallow. Thus, although deeply forked tails seem to be associated with heavier and longer feathers, shallowly forked tails do not always give rise to lighter and shorter feathers. Thomas (1993) showed that the aerodynamic drag and, therefore, the cost of an elongated tail, is proportional to its area. He noted that in assessing the cost of a tail, tail area will be a more reliable cue than tail length. Although the aerodynamic load predominates, feathers also represent part of the load that the tail muscles have to move upon contraction. Therefore, it should not be assumed that tail shape and tail area are the only variables affecting the cost of flight. For a given tail shape (e.g. triangular when spread),

heavier feathers will be more costly to move, unless there are other structures that compensate for the cost of increased loads. Our results suggest the existence of anatomical differences (larger muscular support; see below) that compensate for the cost of increased loads.

Compared with Barn Swallows and Common House-Martins, the depressor caudae muscle is significantly shorter in Bank Swallows (Table 3). Considering the origin and insertion of this muscle, we can assume that its length is an adequate estimate of the length of the vertebral tail. Among the three species, the Bank Swallow is a short-tailed (skeleton) species, whereas both the Barn Swallow and the Common House-Martin are long-tailed species (Fig. 3D).

On the basis of mechanics, the relationship between the magnitude of the muscle force and its position is inherent in the concept of mechanical advantage of the muscle. If the magnitude of the muscular force is held constant, its torque depends upon the length of its moment arm. Hence, insertion of the muscles farther away from the articulation is advantageous for muscles applying a static force against a resistance (Bock 1974). The Common House-Martin and the Barn Swallow, with longer skeletal tails, have enhanced effectiveness of those tail muscles acting around the pelvic joint (fulcrum of the system); that is, M. lateralis caudae, M. pubocaudalis externus, and M. pubocaudalis internus. Therefore, without incurring any extra cost, both species can have longer and/or heavier tail feathers than the Bank Swallow, which is consistent with our results.

In long-tailed (in skeleton) species, muscles acting on the line of the tail should be able to develop more force, because the tail represents the lever arm of the system for such muscles. Our results demonstrate this to be the case for the depressor caudae muscle. It is significantly longer in Common House-Martins and Barn Swallows, which are the long-tailed species, than in the short-tailed Bank Swallow. Longer muscles have more deep fibers that are unipennately arranged; thus, the muscles develop greater force upon contraction (Bock 1974).

We also documented significant differences in the length of the pubocaudalis externus and pubocaudalis internus (Table 2, Fig. 3C), both being longest in Common House-Martins but not differing between Bank Swallows and Barn Swallows. For two muscles of equal cross-sectional area (mass in parallel-fibered muscles),

the shorter muscle shortens faster for heavier loads than the longer muscle (Bock 1974). In species that rely heavily on flight for foraging, velocity of performance of tail maneuvers should be of considerable importance for increased foraging efficiency. This is particularly true for the Barn Swallow, where the turning radius can be significantly reduced by depressing the tail at positive angles of attack (Norberg 1994). An increase in the velocity of tail movements can be achieved by decreasing the load (feather mass) or by decreasing the length of the muscles. Our results demonstrate that Common House-Martins follow the former option, whereas Bank Swallows and Barn Swallows follow the latter.

Barn Swallows also differ from the other two species in lacking the tendinous connection between the pubocaudalis internus muscle and pars caudofemoralis of the caudoiliofemoralis muscle. This is a femur-retractor muscle, but it also can act as a tail depressor (Raikow 1985). Norberg (1994) demonstrated that the tail usually operates at positive angles of attack throughout a turn, which implies the action of the muscles pubocaudalis externus and pubocaudalis internus (see Results). The Barn Swallow, lacking the tendinous connection between the pubocaudalis internus and the caudoiliofemoralis muscles, is likely to benefit from lowering and tilting the tail, because the action of the former muscle is totally independent from the latter.

Our results show that among hirundines, anatomical differences exist among species, giving different mechanical advantages to species with different tail shapes. In Barn Swallows, the presumed cost of having a deeply forked tail can be reduced by having longer skeletal support, which increases the mechanical advantage of tail muscles acting around the pelvic joint, and by having shorter tail-depressor muscles, which increase the velocity of tail maneuvers for heavier loads. Therefore, we propose that in assessing the cost of a tail, variables other than tail shape should be considered.

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