Chapter 2
Time's Arrow in the Evolutionary Development of Bat Flight

Rick A. Adams and Jason B. Shaw

Abstract Conceptualizing the evolution of flight in mammals is confounded by a lack of empirical evidence. In this chapter, we quantify functional ontogeny to model the evolution of flight in bats to fill in transitional gaps between a hypothetical nonvolant ancestor and volant descendents. Our data thus far indicate that bats evolved flapping flight mechanics directly with no gliding intermediate forms and that bats most likely evolved from a terrestrial, rather than arboreal, ancestor. We predict that future analysis of locomotor ontogeny in contemporary bats will be instrumental in bridging the significant gaps and discontinuities between fossil, molecular, and mechanical evidence thus far used to interpret flight evolution in mammals.

2.1   Introduction

The evolution of flight in mammals is one of the most compelling events in vertebrate history. Although some fossil evidence and molecular analyses provide insight into how, and possibly where, the evolutionary transition(s) to flight took place, there persist two unresolved central and interrelated questions (1) *Was the ancestor of bats arboreal, semiarboreal, or terrestrial?* (2) *Did flight evolve in bats via an intermediate gliding form or did flapping flight evolve directly?*

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Darwin (1859) proposed that bats evolved from a quadrupedal arboreal ancestor and went through a transitional gliding state that eventually gave rise to true flight. In efforts to visualize an evolutionary pathway from nonvolant ancestor to volant descendant, the tree shrew (Scandentia, *Tupaia glis*) and the colugo (Dermoptera, *Galeopterus variegatus*) frequently became asserted as representative transitional states (Hill and Smith 1984). For example, Allen (1939) wrote about anatomical similarities between tree shrews and the Middle Eocene *Palaeochiropteryx* and wrote that colugos are "almost bat-like in some respects," and Romer (1959) stated "It seems obvious that the bats, essentially insectivores in their beginnings, have been derived from an arboreal insectivorous group…" and also considered colugos illustrative of an "intermediate stage in the evolution of flight." However, tree shrews are not likely demonstrative of an arboreal ancestor for bats because their probable origin (63 mya) coincides with a time when protobats would have conceivably evolved already (Gunnell and Simmons 2005; Janečka et al. 2007) and colugos are no longer thought representative of a hypothetical intermediate but instead as an evolutionary end point for highly derived gliding (Janečka et al. 2007; Norberg 1985, 1987; Simmons et al. 2008). Many researchers, nonetheless, still continue to view bat evolution as beginning with an arboreal insectivore ancestor that transitioned into bats via a gliding intermediate form (see Giannini 2012 for review). The appealing nature and resilience of the arboreal-gliding hypothesis seems to reside in two well-accepted ways in which key evolutionary innovations may arise (1) transitional states leading to highly derived outcomes are commonly incremental and additive and arise over generations, thereby minimizing the degree of deleterious discordance between form and function, and (2) the origin of patagia was for an established and related mode of locomotion and has easily provided the foundation for co-option into a flapping wing for powered flight (although see Speakman 1999, 2001 for an alternative hypothesis).

Some researchers have argued conversely that bats evolved flapping flight directly with no gliding intermediate (a more punctuated scenario). Moody (1962) asserted that "gliding does not provide the means of entering the flying insectivorous niche" and Jepson (1970) wrote "…no eutheres or the 'flying' marsupials are known to forage or eat while volplaning, the whole function of the glide seems to be transportation." Perhaps most damning of the arboreal-gliding-intermediate hypothesis is that empirical tests on gliding squirrels revealed that transitions from efficient gliding to flapping flight would be severely confounded and unlikely to succeed (Bishop 2008). There is also no fossil evidence showing that gliders of any vertebrate group transitioned to powered flight (Grande 1994; McMillan et al. 2006; Wilf 2000). However, some researchers have shown mathematically plausible aerodynamic models for the transition from gliding to flight, and thus the potentiality remains (Dudley et al. 2007; Norberg 1985).

If a gliding protobat did indeed exist, some have suggested that it may have been omnivorous or herbivorous thereby avoiding the improbable nature of aerial hawking of insects while gliding (Ferrerezi and Giménez 1996; Jepson 1970; Padian 1987; Speakman 2001). Although some Paleocene-age jaw fragments with frugivorous teeth were originally thought to be from bats (Mathew 1917), this has been

challenged (Storch et al. 2002), and teeth of the earliest identifiable bat fossils are tribosphenic, matching those of Early Tertiary insect-eating mammals (Jepson 1966; Rose 2006; Simmons et al. 2008).

Dudley et al. (2007) contends that the many independent lineages leading to the plethora of contemporary vertebrate gliders are strong, albeit indirect, support for the gliding-intermediate hypothesis. However, an equally valid argument would suggest that the existence of mammalian gliders from at least nine independent origins (Jackson 2000; Meng et al. 2006; Scheibe and Robins 1998; Stortch et al. 1996) would have likely given rise to more than a single origin of flight if gliding was an inherent intermediate state.

The goal of this chapter is to integrate baseline data on the ontogeny of flight with likely evolutionary scenarios. We focus on four underlying principles (1) *presence of the past*, that contemporary species retain developmental locomotor pathways laid down during earlier phyletic evolution; (2) *minimize highly risky (maladaptive) behaviors*, selection favors behaviors that reduce the probability of mortality during ontogenetic and evolutionary transitions; (3) *locomotor stability*, selection favors those individuals with the best locomotor skills during ontogeny and evolution; and (4) *Occam's Razor*, when there are two competing hypotheses that make exactly the same predictions, the simpler one is the better.

Descriptive ontogeny has been well documented for several bat species (see Kunz and Parsons 2009 for review). Instead, in this chapter, we pursue a *functional* evo-devo perspective (Breuker et al. 2006) in hopes of providing a more integrative, empirically based blueprint for flight evolution. We use high-speed video to observe previously unnoted details in the ontogeny of flight and tie these data in with molecular and fossil estimates for flight evolution in bats.

2.2 Stability of Gliding Versus Flapping Flight

Flapping flight is commonly considered to be less aerodynamically stable than is gliding (Brown 1953; Maynard Smith 1952; Weis-Fogh 1973), but others argue using mathematical models that neither is inherently less stable than the other (Taylor and Thomas 2002; Norberg 1990). Whatever the case, the transition from nonvolant to volant form, both ontogenetically and evolutionarily, would require minimizing maladaptive discordance between form and function (Norberg 1990). Inherent control of roll, pitch, and yaw angles during gliding or powered flight (Fig. 2.1) must be maintained and is governed by an individual's ability to passively induce opposing forces to deviations in the angles of rotation and to serially dampen out oscillations that would perturb the intended flight trajectory (Maynard Smith 1952).

Flight kinematics in bats is complex because each wing has typically 15 joints that are active throughout a wingbeat cycle. In addition, highly flexible metacarpal and phalangeal joints are capable of hyperextension, and the distal phalanges of digits 2–5 are usually cartilaginous producing highly flexible wing tips (Swartz and
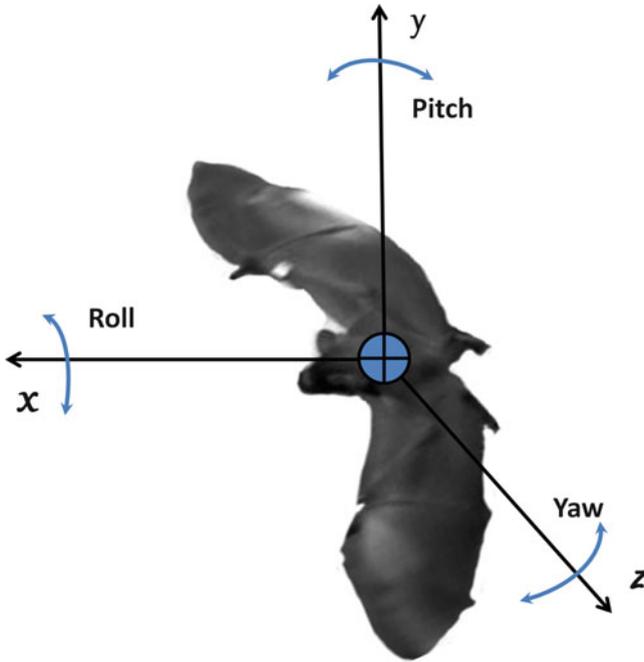
Fig. 2.1 During flight or gliding, the animal is free to rotate about, or translate along, each of three orthogonal axes originating at the center of gravity marked by the *blue circle*

Middleton 2008) that bend and twist in unprecedented ways (Norberg 1990). Clearly the evolution and ontogeny of bat flight is challenging anatomically, physically, and behaviorally.

2.3 Growth and Development of Bat Wings

Shaw (2011) quantified ontogeny of flight morphology in two phyllostomids (*Artibeus jamaicensis* and *Carollia perspicillata*). After standardizing for differences in body size, newborns of the larger bodied *A. jamaicensis* were significantly less developed than were newborns of *C. perspicillata* in the following characters: birth mass; area of wing surface, armwing, and handwing; as well as length of forearm, total wing, armwing, and handwing.

Wing loading and aspect ratio developed similarly in the two species in that as aspect ratio increased, wing loading decreased throughout the first half of development with just the opposite trends during the second half of ontogeny. Curiously, the relationship between these variables is less symmetrical in *A. jamaicensis* than in *C. perspicillata* (Fig. 2.2), and the relationship between the growth and development of the armwing (providing major lift and power) and the handwing (providing
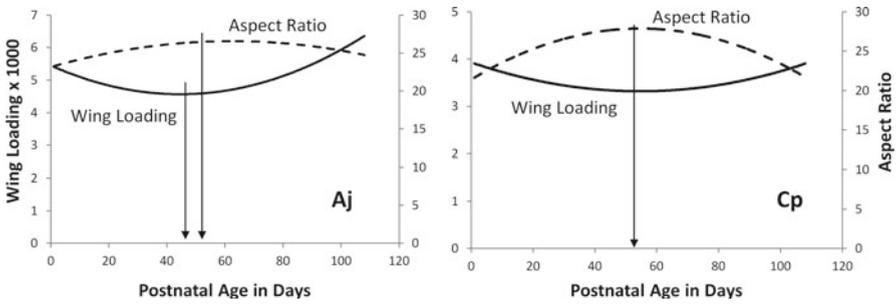
Fig. 2.2 Relationship between changes during ontogeny of aspect ratio (*dotted line*) and wing loading (*solid line*) for *Artibeus jamaicensis* (Aj) and *Carollia perspicillata* (Cp)
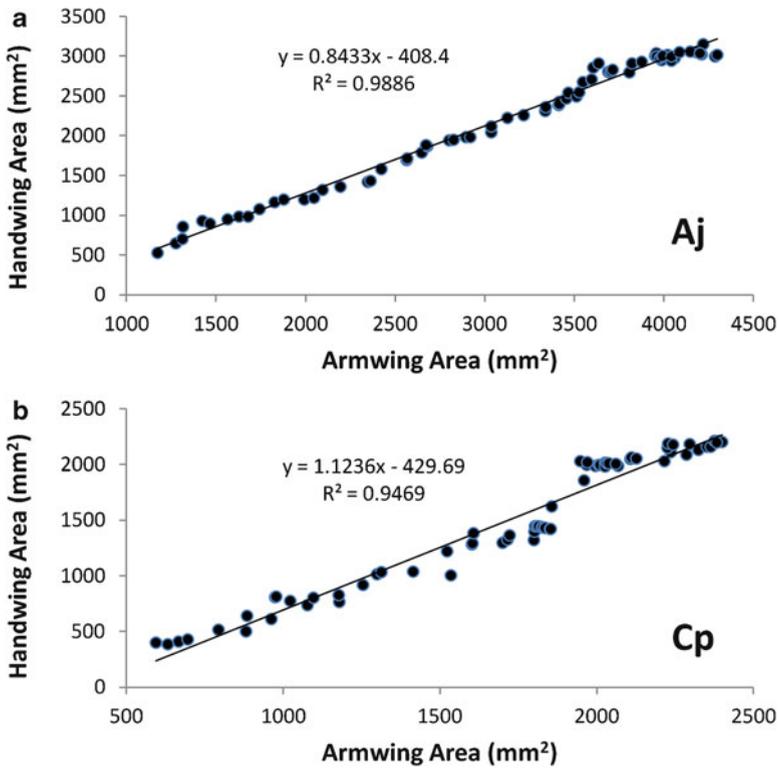

Fig. 2.3 Regression plot of armwing area against handwing areas for (**a**) *A. jamaicensis* and (**b**) *C. perspicillata*

control and maneuverability) is more highly correlated and linear in the larger bodied *A. jamaicensis* (Fig. 2.3).

The shape of the wing tips (wing area ratio/wing tip length ratio – wing tip area ratio) affects maneuverability and thus agility in bats (Norberg et al. 2000).
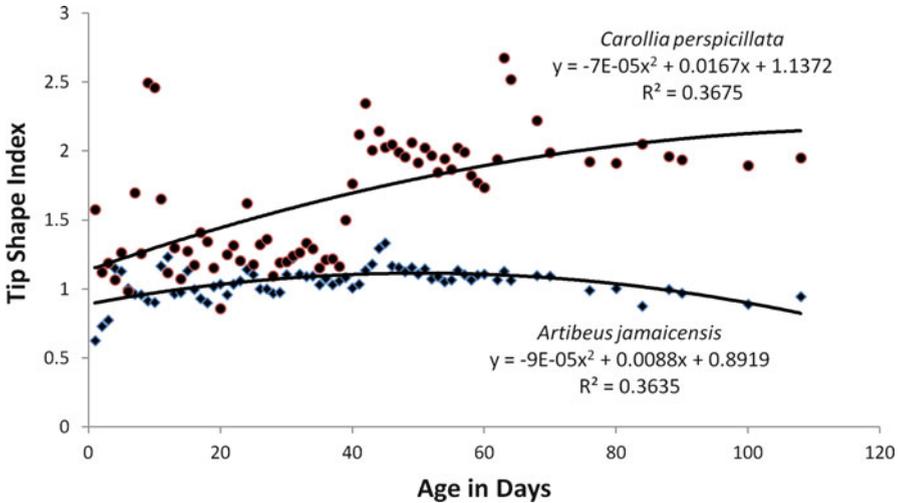
Fig. 2.4 Regression plot of tip shape index for *A. jamaicensis* (*diamonds*) and *C. perspicillata* (*circles*)

Juvenile *A. jamaicensis* showed much tighter variation in wing tip growth and development ($\bar{x} = 1.05$, sd = 0.136) than did *C. perspicillata* ($\bar{x} = 1.64$, sd = 0.44) (Fig. 2.4). Furthermore, proportional changes between the handwing and armwing areas showed tighter correlation in *A. jamaicensis* (Fig. 2.3) which may be a consequence of higher gravitational force (Force = *MA*) acting as a greater selective influence due to consistently higher body mass during ontogeny (Fig. 2.5). Moreover, the asymmetrical relationship between wing loading and aspect ratio in *A. jamaicensis* (see Fig. 2.2) may also be body size related.

2.4 Ontogeny of Flight in Bats

Powers et al. (1991) quantified flight abilities of known-age little brown bats (*Myotis lucifugus*) using a trapdoor and drop box and categorizing four flight stages: *flop*, vertical descent with no flapping and no horizontal displacement; *flutter*, wing motion with no horizontal displacement; *flap*, wing motion resulting in horizontal displacement (20–200 cm), but no sustained flight; and *flight*, sustained with adult-like maneuverability. They observe first wing flapping at day 10, short horizontal flights at day 17, and sustained flight at day 24.

However, with the use of high-speed video taken on newborn of our two species of fruit bats, we revealed that individuals are capable of flapping their wings immediately after birth. Thus, we redefined Powers et al. (1991) *flop* stage as falling to the pad with <3 wing flaps over the 1 m descent and the flutter stage as >3 wing flaps with no horizontal displacement. We found that both species followed the same pattern during the early stages of flight development (flop and flutter) and there were no significant differences in the age at which fluttering began.
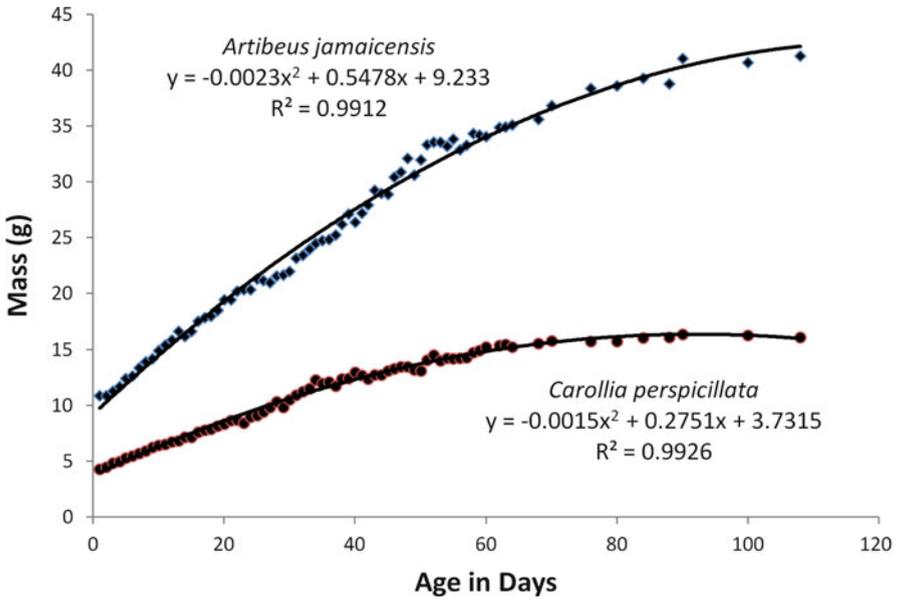
Fig. 2.5 Polynomial growth rate curves for *A. jamaicensis* and *C. perspicillata*
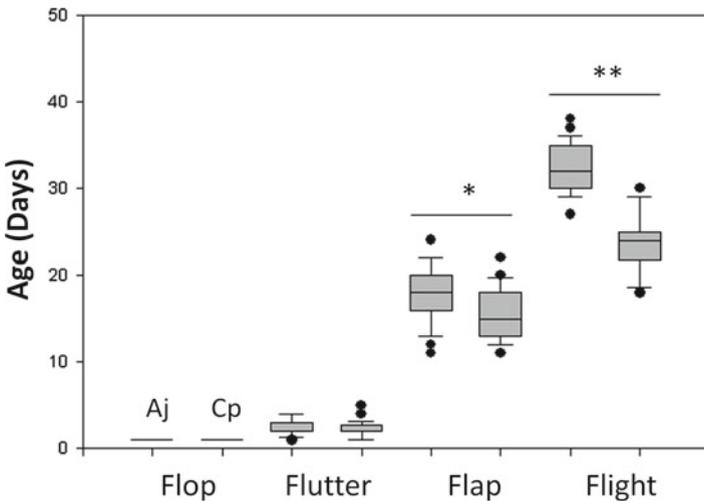

Fig. 2.6 Mean (±SD) age at first observation of each flight development category. *Left boxes* Aj=*Artibeus jamaicensis* and *right boxes* Cp=*Carollia perspicillata*. Wilcoxon Rank Sum test *P=0.01, **P=0.001

However, there were significant differences between species in mean age at which later flight stages came on-line (flapping and flight), with *C. perspicillata* showing earlier aptitude (Fig. 2.6) and beginning to fly on less developed wings than did *A. jamaicensis* (Table 2.1). There was no significant difference in the number of days

Table 2.1 Mean proportions of adult body mass, forearm length, wingspan, and wing area of each species with initial flight capacity

Variable	Artibeus jamaicensis (%)	Carollia perspicillata (%)
Body mass	59	56
Forearm	94	82
Wingspan	90	82
Wing area	77	67
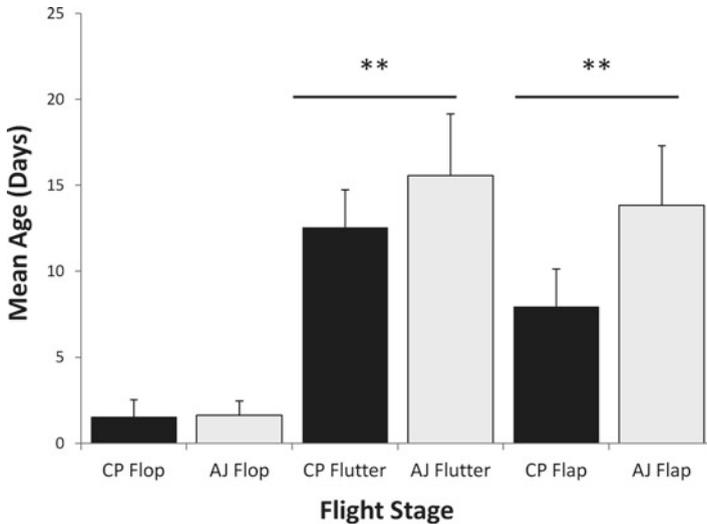
Fig. 2.7 Mean (±SD) days spent within each developmental flight category. *Black bars* represent *A. jamaicensis* and *gray bars* represent *C. perspicillata.* **$P \leq 0.001$

each species spent in the flop stage, but *A. jamaicensis* juveniles spent significantly more time in flutter and flap stages (Fig. 2.7).

Shaw (2011) quantified agility of 20 *A. jamaicensis* and 15 *C. perspicillata* juveniles by flying them through a flight maze constructed of four rows of offset 1 m long, 5 mm diameter dowel rods hung on string. Spacing between dowels was set at the full wingspan of each individual and then adjusted to 75 % and 50 % of an individual's wingspan for successive trials. Agility was quantified by frequency of dowel rods contacted during each trial, and mean juvenile agility was compared with mean agility of five adults of each species.

Thirty five-day-old juvenile *A. jamaicensis* were able to maneuver through the maze at the full wingspan setting with agility equal to adults. The performance of juveniles when dowels were set at 75 % wingspan spacing was equal to adults at 45 days and at 50 % wingspan spacing at 65 days of age. Juvenile *C. perspicillata* were able to successfully maneuver the course at full wingspan dowel spacing with adult agility at 30 days postnatal development, at 75 % wingspan at 40 days, and at 50 % wingspan at 50 days. Differences between the two species in age-specific agility relative to adults were not apparent at the full wingspan setting; however, at 75 % of
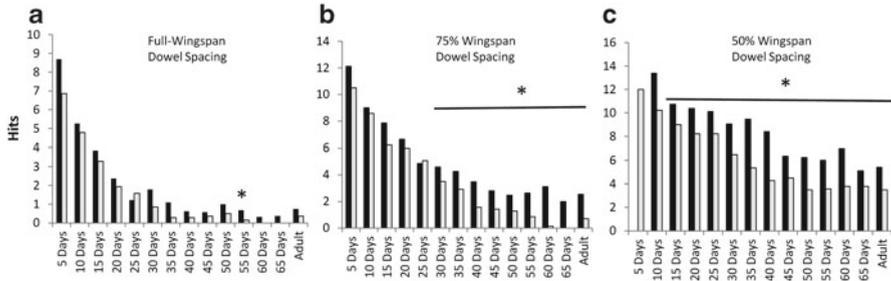
Fig. 2.8 Number of dowel rod contacts at different ages of postflight agility for *C. perspicillata* (*black bars*) and *A. jamaicensis* (*open bars*). (**a**) Dowel rods spaced at full wingspan. (**b**) Dowel rods spaced to 75 % of wingspan. (**c**) Dowel rods spaced at 50 % of wingspan

wingspan, there was a significant difference between the two species from day 30 onward and at 50 % of wingspan from day 10 onward (Fig. 2.8).

Although agility at any age is controlled, in part, by wing loading and aspect ratio, muscle development also contributes greatly to flight control and stability. Locomotor muscles in mammals are composed of up to three different fiber types, belonging to motor units that have distinct functional properties controlling various performance parameters. Several classification paradigms are based on the properties of myosin heavy chains broken down into type I, type IIa, and type IIb motor units (Brooke and Kaiser 1970; Guth and Samaha 1969, 1970). In bats, the pectoralis muscles are used for sustained forward motion, specifically performing the downstroke of the wings (Hermanson and Altenbach 1981, 1985; Vaughan 1970), whereas the acromiodeltoideus muscles are one of a set of paired abductor accessory flight muscles that are active throughout the upstroke (Hermanson and Altenbach 1985).

Pectoralis and acromiodeltoideus muscles in adult little brown bats (*M. lucifugus*) were composed entirely of fast-twitch fibers by the time of weaning (Powers et al. 1991). Growth and development of the pectoralis in juvenile *C. perspicillata* was similar to *M. lucifugus*, whereas in *A. jamaicensis*, what begins as 90 % fast-twitch fibers switches to 30 % slow twitch in the flap stage and 60 % slow twitch in adults. Shaw (2011) hypothesized that the increase in slow-twitch fibers during ontogeny in *A. jamaicensis* may afford greater efficiency for sustained commuting flight in open habitats by adults.

Flight muscle development and agility of two species showed a consistent pattern wherein the ability to successfully maneuver the maze was dependent upon the percentage of (Fig. 2.9) and diametrical growth (Fig. 2.10) of pectoralis fast-twitch muscle fibers (PFT) rather than those of the acromiodeltoideus (DFT). Curiously, diametric growth of both the pectoralis and acromiodeltoideus fast-twitch fibers appears to be equally invested in increasing agility for *A. jamaicensis* (Fig. 2.10), whereas in *C. perspicillata*, agility appears most related to pectoralis development (Hermanson and Altenbach 1981, 1985; Vaughan 1959, 1970).

As juveniles began to fly, they had grown to similar ratios of mean adult body mass for their respective species. However, the relationship between body mass and wing dimensions was quite different between the two species on the first day of
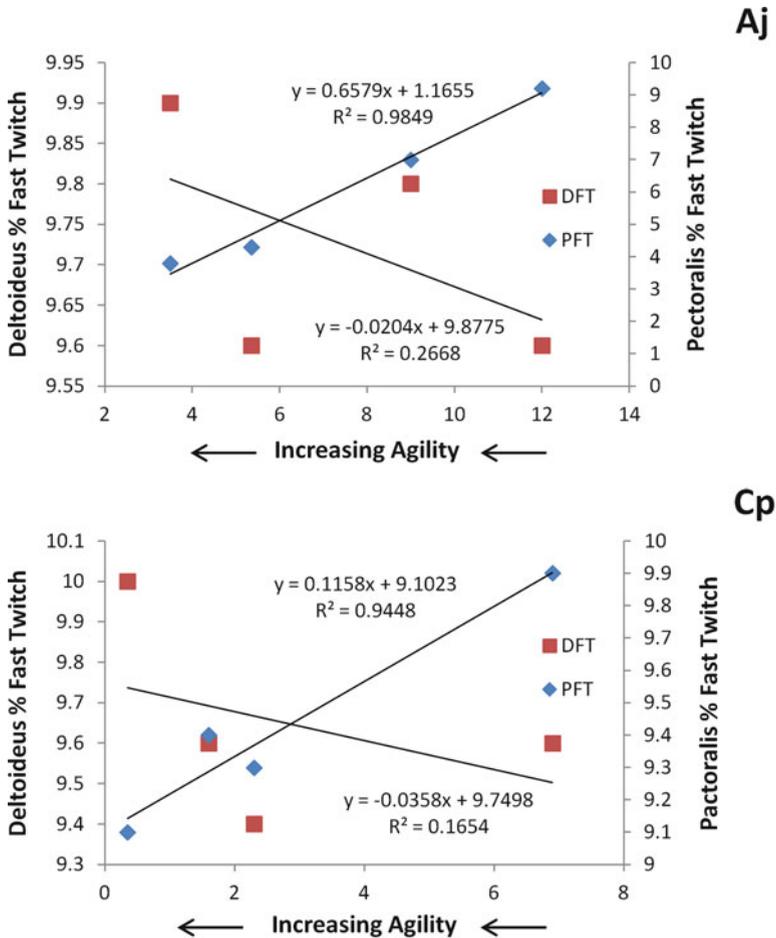
Fig. 2.9 Development of fast-twitch fibers in the major flight muscles as compared to increasing agility of *A. jamaicensis* and *C. perspicillata*. In both species, agility was best correlated with percent maturation of pectoralis fast-twitch muscles. *DFT* acromiodeltoideus fast twitch, *PFT* pectoralis fast-twitch muscles

flight. In fact, *C. perspicillata* begins flying on quite stubby wings compared to *A. jamaicensis* and yet has the same agility (Table 2.1).

2.5 Evo-Devo Modeling of Derived Morphologies

There is a long and deep history between development and evolution that supports the underlying premise that derived morphologies are additive rather than substitutive. Perhaps Garstang's (1922) statement "Ontogeny does not recapitulate
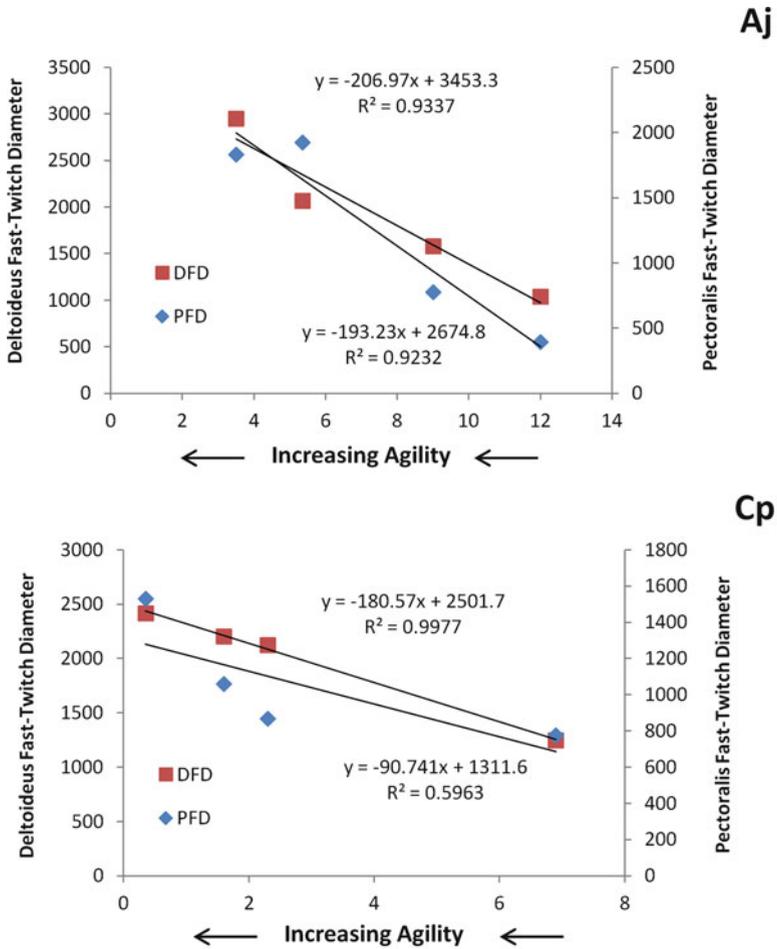
Fig. 2.10 Plots of mean diameters of the pectoralis and acromiodeltoideus muscles as related to agility in *A. jamaicensis* and *C. perspicillata*. Abbreviations as in Fig. 2.9

phylogeny, it creates it" says it best. In kind, Liem and Wake (1985) stated "As far as morphological change is concerned, evolution acts by altering development." Despite the simplicity of these two notions, a coherent understanding has been confounded by the inability to sometimes track the ontogeny of derived morphologies (Swan 1990; True and Haag 2001).

"Deep homology," a product of shared genetic apparatus to form similar structures among phylogenetically disparate organisms (i.e., dipteran wings and tetrapod limbs), shows that historical continuity may reside cryptically within complex regulatory circuitry (Baguñà and Garcia-Fernández 2003; Jablonka and Lamb 1998; Shubin et al. 2009). Innovation, it appears, is a product of modifications of conserved genetic networks rather than the evolution of novel genes or genetic pathways

(see reviews in Brakefield 2006, 2011; Shubin et al. 2009). For example, regulatory constraints and co-option of the trunk segmentation collinear mechanism appear to have imposed an anterior-posterior polarity in tetrapod limbs at their first appearance, and, although hard to track, this regulation is still present throughout modern mammals (Kmita et al. 2005; Tarchini et al. 2006; Young and Badyaev 2007). A relatively new focus on how modified developmental pathways result in evolutionary divergence includes the epigenetic aspects of environmental sensitivity (see reviews in Hall et al. 2003; West-Eberhard 2003) wherein increased developmental plasticity produces novel morphologies with environmental selection acting on the new phenotype or even as an inducing mechanism (Young and Badyaev 2007).

Much of skeletal development is epigenetic (Goldberg et al. 2007; see also Chap. 1), and differential expression of bone morphogenic protein (BMP) is a primary mechanism in controlling cartilage and bone formation. Typically these changes are attributed to mutations in the regulatory regions of BMP pathways (Albertson and Kocher 2006; Sears et al. 2006; Terai et al. 2002; Chap. 1); however, we know comparatively little about how extrinsic stimuli affect development (see West-Eberhard 2005 for review).

2.6   Evo-Devo Modeling of Mammalian Locomotor Patterns

Because adaptive behaviors require functional links among morphogenetic modules both developmentally and evolutionarily, quantifying how locomotion behaviors come on-line during ontogeny can act as a surrogate for understanding ancestor-descendent transitions (Bertossa 2011; Müller 1990, 2007; Oster et al. 1988; Raff 2007). The wide diversity of locomotion in mammals all stem from a basal ancestor and develop through the ancestral ontogenetic pathways that stretch back to the origin of terrestrial vertebrates 360 mya. For example, Westerga and Gramsbergen (1990) found that newborn rats crawled with their ventrum in contact with the floor and after day 11, a gradual transition to free walking took place during which paw strikes were initially plantigrade with flexed interphalangeal joints producing wobbly gait with lateral bending of the spine similarly to that of the first terrestrial vertebrates (Ischer and Ireland 2009; Romer 1959; Williams 1981).

During ontogeny, gait kinematics of the adult tree shrew (*T. glis*) was surprisingly similar to the precocial terrestrial cui (*Galea musteloides*) even though as adults kinematic distinctions are easily evident (Schilling and Petrovitch 2006). Even the development of bipedal locomotion in the jerboa (*Jaculus orientalis*) begins with the typical neonatal condition of walking on hind limbs and forelimbs of equal length with bipedal locomotion not arising until day 47 (Eilam and Shefer 1997), and the overall progression of ontogenetic events followed those of less derived quadrupedal rodents (Eilam 1997; Eilam and Shefer 1997). In black-tailed jackrabbits (*Lepus californicus*), neonates have short hind limbs for walking prior to the onset of rapid elongation and quadrupedal saltation (Cretekos et al. 2008; Eilam 1997). A comparison between rodent species that use a specialized half-bounding

gait (*Chinchilla lanigera* and *Oryctolagus cuniculus*) and two unspecialized species (*Rattus norvegicus* and *Monodelphis domestica*) showed that all four groups shared common developmental patterns (Lamers and German 2002).

Ferron (1981) compared ontogeny of locomotion in four squirrel species [*Spermophilus columbianus*, *S. lateralis* (both terrestrial), *Tamiasciurus hudsonicus* (arboreal), and *Glaucomys sabrinus* (arboreal/gliding)] and found that all four followed the same patterns of locomotor development, but in the gliding species *G. sabrinus*, climbing behavior occurred 2 weeks earlier than in the others. Indeed, comparative locomotor development across many mammal taxa (Didelphidae, Rodentia, Lagomorpha, Hyracoidea, Artiodactyla, Scandentia, and Primates) shows that ancestral morphologies and gaits consistently precede the appending of derived morphologies and behaviors (Fischer et al. 2002; Schilling 2005; Schilling and Petrovitch 2006; Witte et al. 2002).

2.7   Gliding Versus Direct Flapping Flight Hypotheses

Studies of the ontogeny of flight are central in uncovering how vertebrate wings evolved (Dial et al. 2008). Foundational modular integration is a key attribute for both the ontogeny and evolution of form and function and must be maintained during transitional states (Breuker et al. 2006). Using high-speed videography, we have shown that newborn bats just a few hours old have the reflexive behavior of wing flapping even when their body orientation is not conducive for flight (Fig. 2.11). Clearly then the basic mechanics and neurology for reflexive flapping are laid down before birth, and bats may be similar to rats in which inter-limb coordination occurred at day 20 of a 21-day gestation period (Bekoff and Lau 1980).

Initially, newborn bats only dorsally extended their wings about +45° to the body plane, whereas ventral range of motion was nearly −85°. By day 4, however, the backstroke wing angle was nearly +84°, reflecting the sudden burst in acromiodeltoideus function (represented in Fig. 2.10). When newborn young were dropped

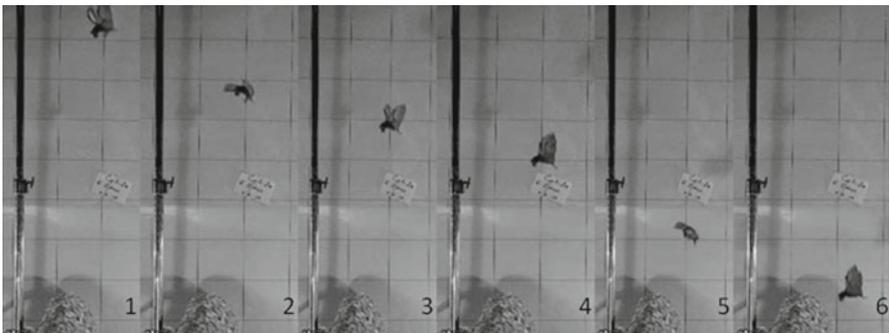**Fig. 2.11**   Hand-dropped 6-day-old *C. perspicillata* exhibits flapping immediately upon release
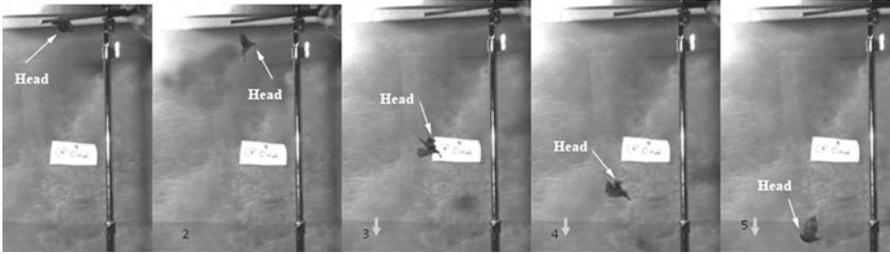
Fig. 2.12 Sequence of 1-day-old postpartum *C. perspicillata* dropped from a drop-stick hanging position. This individual became inverted and unable to reorient its body axis. Although the individual becomes inverted, it flapped its wings throughout the 1 m drop. We interpret this to mean that flapping is an innate reflex
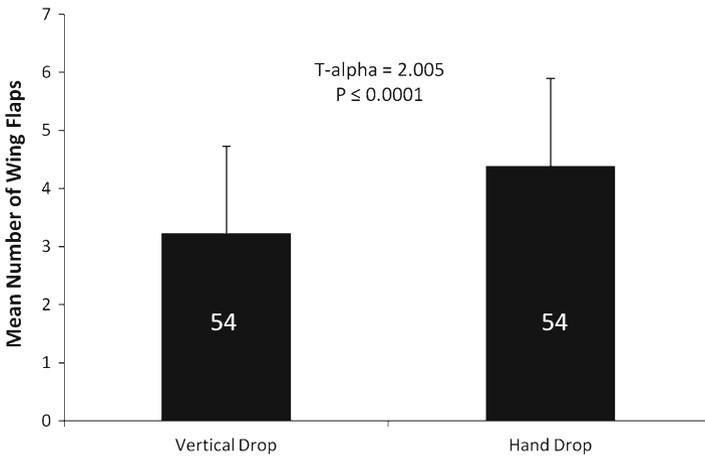

Fig. 2.13 Comparison of number of flaps achieved by preflight juvenile *C. perspicillata* in 54 releases hanging from a rod in a vertical body position versus 54 releases of the same individuals from a handheld horizontal body position. Vertically drop averaged 3.23 flaps (SD = 1.49) versus horizontal drops averaged 4.39 (SD = 1.51)

from a vertically hung position, they had significant trouble controlling body-axis rotations, and on several occasions, individuals that became inverted (were falling upside down) would nevertheless flap their wings until they landed on the soft pad below (Fig. 2.12). We also found that preflight young released with their bodies held horizontally significantly outperformed trials in which the same individuals were released from a hanging position (Fig. 2.13). In addition, flapping performance using the same tests on 18 individuals of *C. perspicillata* from 16.5 to 26.5 days of age showed similar patterns of greater performance when horizontal drops were performed (Fig. 2.14). Thus, control of flapping flight at early developmental stages was gained when individuals did not need to reorient their body axis from vertical to a horizontal flight plane.
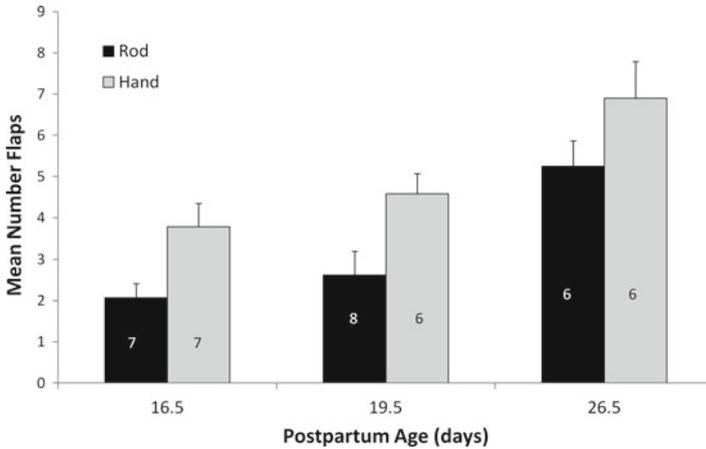
Fig. 2.14 Mean and standard deviations of number of wing flaps during rod- versus hand-drop tests of juvenile *C. perspicillata* at 16.5, 19.5, and 26.5 days of age. *Numbers* in bars indicate number of drops per test. There were significant differences between each category per age, but the degree of significance lessened with age

Fig. 2.15 A 24-day-old *C. perspicillata* lifting off from a horizontal platform on the first day it was capable of flight holds its body axis steady throughout takeoff and subsequent flight. *White lines* represent the horizontal

The first day of sustained flight for juvenile *C. perspicillata* was at 26 days on average, and all were capable of performing horizontal launches from a table top by pushing off at the wrist, resulting in excellent body-axis control during takeoff (Fig. 2.15). However, the same juveniles released from a vertical, hanging position required a free fall of about 0.5 m before orienting the body axis properly (horizontally); struggled to maintain pitch, yaw, and roll control; and commonly did not get to a sustained flight mode. It is certainly conceivable that bats evolved on vertical landscapes such as cliff faces using push-off launches (Caple et al. 1983) from a vertical position (Fig. 2.16). In our tests, we found that push-off launches while hanging on a vertical platform suffer similar mechanical and control challenges to vertical, drop-stick launches (Fig. 2.17).

2.8 From the Cradle to the Air

Much of what we know about the origin of bats is based on fossils from two regions: Messel, Germany, and the Green River Formation, Wyoming, USA. Although it is currently impossible to determine the geographic origin or "cradle"
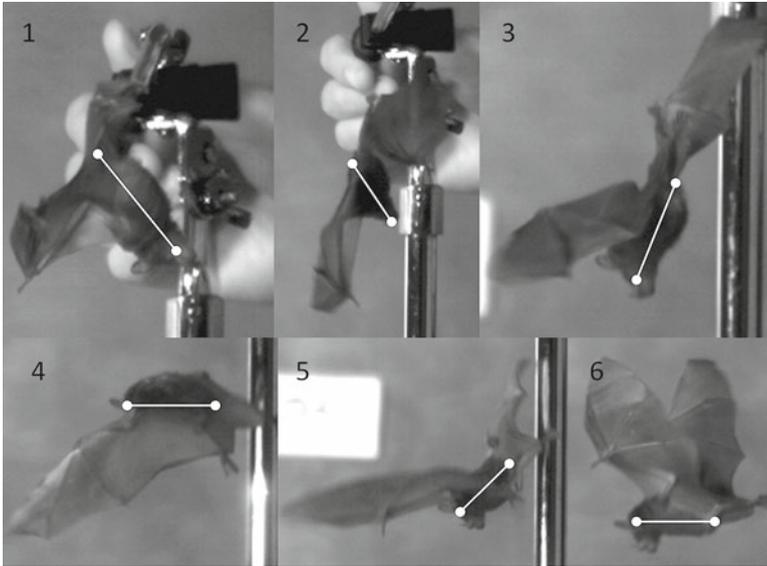
Fig. 2.16 Vertical drop sequence (1–6) of a 31-day-old *C. perspicillata* shows a lack of control in body orientation (pitch, roll, and yaw) when shifting from a vertical to a horizontal flight axis. *White lines* here mark the approximate body axis

Fig. 2.17 Push-off launch from vertical platform of 31-day-old *C. perspicillata*. Individual struggled to control body-axis pitch. *White lines* mark body axis

of bat evolution, both fossil and molecular data point to a Laurasia origin, possibly North America, sometime near the K–T boundary (~64 mya) (Smith et al. 2012; Teeling et al. 2005). However, molecular analysis has also indicated that a split of Chiroptera into two groups named Yinpterochiroptera (rhinolophids and pteropodids) and Yangochiroptera (all other bats) occurred at about 55–57 mya (Teeling 2009), and this does not appear to align with the early fossil bats. Analysis on the genomes of *Pteropus alecto* and *Myotis davidii* supports a divergence of bats from the Laurasiatheria as early as 88 mya (Zhang et al. 2013). However, the most comprehensive study on the origins of placental mammals and derived groups indicates

the origin of bats at or just after the K/Pg boundary at 65 mya (O'Leary et al. 2013). *Icaronycteris index*, described by Jepson (1966), was considered to be the most primitive instance of a bat, but has since been superseded by the discovery of another fossil bat from the same formation. This new species, *Onychonycteris finneyi*, is larger bodied than other Eocene bats, lacks typical fusions in the ribs and vertebrae, and has claws on all digits of the manus (Simmons et al. 2008). Further, *O. finneyi* has limb proportions that are intermediate between other fossil bats and those of nonvolant climbing mammals such as colugos, a more ancestral character state than *I. index* although occurring at about the same time.

More broadly, comparative morphology indicates that bats are descended from the Archonta (dermopterans, primates, and tree shrews); however, molecular analyses indicate that bats originated from Laurasiatheria, appearing either (a) as a sister group or a basal member of a cetferungulate clade (pholidotans, carnivores, cetaceans, artiodactyls, and perissodactyls) or (b) as a sister group of the eulipotyphlan clade (shrews, moles, and possibly hedgehogs). The consensus being that bats rest within the basal laurasiatheres (see Gunnell and Simmons 2005 for review).

The timing and order in which the major components of the bat wing develop (plagiopatagium, membrane stretching between the body and forearm, i.e., armwing; dactylopatagium, membrane that stretches between digits 2 and 5, i.e., handwing) give insight into the evolutionary sequence of wing evolution. Morphological and molecular investigations of wing formation indicate that the different patagial components that compose a bat's wing develop independently and at different developmental stages in both Microchiroptera and Megachiroptera indicating that the evolution of these structures was also independent and temporally unrelated (Cretekos et al. 2005; Giannini et al. 2006; Weatherbee et al. 2006). Curiously, new research has determined that the wing muscles in bats also have multiple embryonic origins and myogenic sources and that the wing membrane itself regulates wing muscle patterning (Tokito et al. 2012) similar to patagial growth controlling serial length compensation among wing bones (Adams 1998), also shown to occur in *Hipposideros pomona* (Lin et al. 2011).

From a functional perspective, the evolution of flapping flight versus gliding would involve different evolutionary, and thus developmental, arrangement of the patagia (Gardiner et al. 1999). Establishing a gliding morphology would have favored the ontogeny and evolution of a membrane that stretched between the lateral body wall and the forearm (plagiopatagia), thereby producing a flight surface with a small lever arm and turning moment. Conversely, for flapping flight, formation of a dactylopatagium would be favored for maximizing power stroke, turning ability, and orientation control.

2.9 Synthesis

Time's arrow is a concept developed by astronomer Arthur Eddington in 1927 to describe the past to present direction of time (Carroll 2010). Integrating the drastically different arrows of time between ontogeny and evolution has produced

Table 2.2 Concordance hypothesis between developmental stages (based upon data gathered on *C. perspicillata*) and evolutionary stages (based on molecular and fossil evidence)

Ontogeny	Timing	CONCORDANCE			Timing	Historical
Adult	> 60 days	100% wing span	100% adult diameter	High-agility flight	Eocene ~ 52.5 mya	Icaronycteris
Subadult	27-30 days Flight stage	Short/broad low AR 90% adult wing span		Medium-agility flight		Onychonycteris
Subadult	26 days Flight stage	Short/broad low AR 82% adult wing span	69% adult diameter	Low-agility flight	Eocene ~55.5 mya	4th hypothetical descendant
Prevolant juvenile	17 days Flutter stage	Short/broad low AR 63% of adult wingspan	57% adult diameter	Leap-up, flutter over distance	Eocene ~ 56 mya	3rd hypothetical descendant
Prevolant newborn	~ 115 days Flop stage	Dactylo-/ Plagiopatagium 50% adult wingspan	25-51 % adult diameter	Full wing present, leap-up, controlled descent	Paleocene ~ 56.5 mya	2nd hypothetical descendant
3rd Trimester	~ 60 days	Dactylopatagium	< 25% adult diameter	Hand wing present, unknown function	Paleocene ~ 58 mya	1st hypothetical descendant
2nd Trimester	~ Stage 15 46 days	Standard-issue hand plate	none	none	Paleocene ~ 64 mya	Hypothetical Laurasiatherian ancestor
		Wings	Cross-Section Fast-Twitch Muscle	Flight Behavior		

Error bars for estimated evolutionary events may comprise several million years

important insights into how, when, and why key morphological and behavioral innovations transpired (Hall et al. 2003; Smith 2003; Swan 1990), and some would argue that the evolution of adult morphology is little more than the differential success of developmental innovation (Klingenberg 1998; Liem and Wake 1985; Müller 1990).

By evaluating both the timing of significant ontogenetic events in relation to molecular and fossil evidence on bat evolution, we can begin to draw concordances (Table 2.2). Because the fossil record for bats is so poor and in many cases molecular analysis has not been supported by fossil evidence, we use a combination of those aspects of each which do appear to align together. Data from correlations between the rate of speciation and the rate of chromosomal evolution show that extant bats are evolving at a relatively slow rate compared to insectivores, rodents, carnivores, lagomorphs, artiodactyls, and marsupials, but faster than whales. The corrected speciation rate for bats as compared to these other species was determined to be 0.7 new species/lineage per million years (Bush et al. 1977). Of course, speciation rates can vary through space and time, and one would expect key evolutionary innovations to evolve in a punctuated manner with rapid transitional stages (Eldridge and Gould 1977). Furthermore, diversification rates in any lineage likely have not been constant and for bats appear to have responded positively to major environmental events such as shifts in flowering plant diversity rates (Jones et al. 2005).

Because the components of the wing in bats develop separately both in timing and location (Weatherbee et al. 2006), the dactylopatagium, which develops first, was probably the first patagium to evolve in concert with elongation of digits 2–5, forming an incipient wing that appears prenatally on ~day 60 of a ~115-day gestation

period. Evolutionarily, this timing would equate to the Middle Paleocene (~58 mya) and represent an initial hypothetical descendant on the pathway to true flight. The adaptive nature of the proposed dactylopatagium remains unknown, but it has been suggested that such a structure would be useful in capturing insects (Speakman 1999). In our scenario, these could be either ground or flying insects. At birth (~115 days), *C. perspicillata* has both a dactylo- and plagiopatagium and is capable of some controlled flapping upon descent (flop stage). This equates to a second-stage descendent with the capacity to leap up with controlled descent living in the Late Paleocene (~56.5 mya). This may be the first time in evolutionary history that protobats attempted to use their wings for a newly found locomotor mode, flight. From this point onward, selection favored adaptations consistent with further flight development and evolution perhaps to avoid predation as observed in birds (see Heers and Dial 2012 for review). Our third hypothetical descendant living ~56 mya equates to a 17-day-old prevolant juvenile with the capacity to flutter over a distance up to 200 cm to or from vertical surfaces or flapping gently to the ground after jumping upward to catch insects as portrayed by Caple et al. (1983). We estimate that such jumping and fluttering behavior would not be sustainable in distance or altitude due to the lack of fast-twitch muscle support, predicted by ontogeny to be only about 25 % of adult capacity. The fossils *Onychonycteris* and *Icaronycteris* appear to be steps along the evolutionary continuum with the former being an ancestral state. These fossils, both living forms ~52 mya, appear to equate with the ontogenetic transition from late subadult to adult flight morphology, mechanics, and agility. Late-stage subadult *C. perspicillata* are capable of sustained flight, but lack some agility, and we hypothesize that this flight behavior is representative of what would be expected in *O. finneyi*, apparently a less agile flyer than was *I. index* due to its higher wing loading and small wing tips (Simmons et al. 2008). As mentioned, *C. perspicillata* began flying on quite stubby wings with underdeveloped flight muscles that seem to represent a more ancestral flight morphology similar to that depicted in *O. finneyi* (Simmons et al. 2008). However, *O. finneyi* had body-size dimensions similar to *A. jamaicensis*, meaning that higher flight speed would be required to stay aloft and thus consequently lower agility. Perhaps *O. finneyi* represents an evolutionary benchmark that depicts a time in bat evolution when flight was entering an innovative phase allowing for aerial insectivory.

2.10 What Bats Inherited Versus Derived

Much focus on the derived characters of bats has involved the serial order in which such innovations came about over evolutionary time (see Gunnell and Simmons 2012 for review). It seems to us that perhaps in some of these cases, the traits that are being assigned as evolving in bats may instead have been inherited in basal form from their common ancestor. We propose that recent hypotheses on the evolution of bats have confused inheritance with derivation of form and function. A prima facie

example is the argument concerning which came first in bats, flight or sonar (Simmons et al. 2008; Veselka et al. 2010). Recent research has shown quite unequivocally that the use of ultrasound is quite common among small mammals (Blumberg 1992; Kalcounis-Rüppell et al. 2006). Most relevant to the evolution of bats is the fact that sonar is used by contemporary species in the genus *Sorex* (Siemers et al. 2009) and *Blarina* (Tomasi 1979). In addition, it appears that the use of ultrasound in these shrews has evolved to a state allowing for its use in navigation and potentially the identification of objects in the environment. Thus, it seems more probable to us that bats inherited primitive sonar from their ancestor and built upon this foundation to produce the exquisite echolocation exhibited by extant species, rather than the likelihood that bats reinvented this ability from scratch. Likewise, other aspects commonly associated with bat evolution such as nocturnal activity, high metabolic rates, and reduced visual acuity were inherited from a shrewlike ancestor. Other aspects of bat natural history seem clearly to be derived by bats and may be directly linked to the evolution of flight such as longer gestation periods that facilitate the growth and development of wings and lengthening of life spans hypothesized to be a consequence of the extensive use of torpor and hibernation (see Barclay and Harder 2003 for review).

2.11   Conclusions

The hypothesized concordance between the timing of ontogenetic events and those of important evolutionary innovations we propose in this chapter provides a foundation for further testing. Our ontogenetic analysis in relation to our four basic principles stated in the introduction thus far supports that, similar to other mammals with derived morphologies and locomotion, bats pass through ancestral locomotor stages before acquiring the morphology and functional capacity for flight. We found that the most stable platform for the ontogenetic transition from nonvolant to volant form indicates that push-off launches from a horizontal platform are best for maintaining body-axis control during takeoff (Fig. 2.18). A horizontal takeoff also entails minimizing risky behavior as failures would result in minimal fall distances. Finally, our ontogeny data support the direct evolution of flapping-powered flight because juveniles with wings not yet developed enough to support flight exhibit reflexive flapping behavior when in free fall. The ontogeny and evolution of direct flapping mechanics also embraces Occam's Razor in that the succession from nonvolant to volant form is accomplished by modest transitional stages rather than dramatic specialized adaptations and behaviors associated with transitions from scansorial and/or pendular arboreal locomotion to gliding ability and then flapping flight. Much more data and understanding about the ontogeny of locomotion in bats including walking, climbing, and early flight kinematics with integration of ecology and behavior (Adams 2008; Adams and Pedersen 2000) are greatly needed to provide empirical evidence for the origin of flight in mammals.

Fig. 2.18 Horizontal platform launch of the vespertilionid bat *Myotis evotis* filmed at 300 frames per second

Our proposed scenario, however, does fall short in understanding why patagia would evolve in protobats if not for gliding first. Speakman (1999) suggested that dactylopatagia evolved initially for insect capture during reach hunting from arboreal perches, and thus it is possible that reach hunting may have evolved in a ground-based or semiarboreal ancestor as well. However, it is also feasible that a semiaquatic ancestor among early insectivores with webbed digits provided a suitable ancestor. Recent findings that "walking" bats, such as mystacinids, had ancestral origins as early as 51 mya, in a time and place where numerous ground-based predators occurred (Hand et al. 2009), offer further evidence that terrestrial locomotion in bats may not be a derived condition, but rather an ancestral condition rooted in all bats.

In addition, new evidence that the tail-membrane in vespertilionid bats may help with thrust during takeoffs from a horizontal position (Adams et al. 2012) might also be part of this evolutionary picture. Because *O. finneyi* had a substantial calcar and thus an extensive tail-membrane, it, and earlier bats, may have used tail-thrust to help during ground launches. The addition of earlier fossil evidence for transitional states will be central to our further understanding for the evolution of bats. However, using ontogeny to bridge the current gaps in time's arrow from past to present, ancestor to descendent, deepens the discussion and refocuses the intellectual path forward.

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