Corrigendum

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There was an error published in *J. Exp. Biol.* **215**, 480-496.

On p. 481, the gestation length for *Petaurus breviceps* was incorrectly stated to be 16 weeks. The correct gestation length is 16 days. The authors apologise for any inconvenience that this error may have caused but assure readers that it does not affect the results or conclusions of the paper.

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RESEARCH ARTICLE

# Kinematics of quadrupedal locomotion in sugar gliders (*Petaurus breviceps*): effects of age and substrate size

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## SUMMARY

**Arboreal mammals face unique challenges to locomotor stability. This is particularly true with respect to juveniles, who must navigate substrates similar to those traversed by adults, despite a reduced body size and neuromuscular immaturity. Kinematic differences exhibited by juveniles and adults on a given arboreal substrate could therefore be due to differences in body size relative to substrate size, to differences in neuromuscular development, or to both. We tested the effects of relative body size and age on quadrupedal kinematics in a small arboreal marsupial (the sugar glider, *Petaurus breviceps*; body mass range of our sample 33–97 g). Juvenile and adult *P. breviceps* were filmed moving across a flat board and three poles 2.5, 1.0 and 0.5 cm in diameter. Sugar gliders (regardless of age or relative speed) responded to relative decreases in substrate diameter with kinematic adjustments that promote stability; they increased duty factor, increased the average number of supporting limbs during a stride, increased relative stride length and decreased relative stride frequency. Limb phase increased when moving from the flat board to the poles, but not among poles. Compared with adults, juveniles (regardless of relative body size or speed) used lower limb phases, more pronounced limb flexion, and enhanced stability with higher duty factors and a higher average number of supporting limbs during a stride. We conclude that although substrate variation in an arboreal environment presents similar challenges to all individuals, regardless of age or absolute body size, neuromuscular immaturity confers unique problems to growing animals, requiring kinematic compensation.**

Key words: ontogeny, kinematics, quadrupedalism, marsupials, arboreality, gait.

## INTRODUCTION

Young animals move in the same habitats as adults but face unique disadvantages in terms of their ability to locomote effectively. Compared with adults, juvenile animals not only are smaller in body size but also have an immature musculoskeletal system, reduced sensorimotor integration and rapidly changing body proportions (Carrier, 1996). Without a means to circumvent these deficits, juveniles may not be able to compete for food, are more susceptible to predation, and thus might not survive to reproductive age (Herrel and Gibb, 2006). Not surprisingly, laboratory and field-based research on vertebrates has revealed that juveniles are not simply scaled down versions of adults with respect to morphology and locomotor behavior. Rather, numerous ontogenetic locomotor studies have demonstrated that juveniles exhibit both anatomical and behavioral mechanisms that compensate for limitations on locomotor performance and shifting body proportions (e.g. Carrier, 1983; Carrier and Leon, 1990; Carrier, 1995; Main and Biewener, 2004; Main and Biewener, 2006; Main and Biewener, 2007; Young, 2009a). For example, the relatively large hands and feet of juvenile mammals compared with those of adults provide stability and, in arboreal contexts, permit navigation of adult-sized substrates (Jungers and Fleagle, 1980; Ravosa et al., 1993; Turner et al., 1997; Lammers and German, 2002; Raichlen, 2005b; Lawler, 2006; Schilling and Petrovitch, 2006; Young, 2009a; Heard-Booth and Young, 2010). Juvenile mammals compensate for limited muscle mass with relatively long muscle lever arms compared with those of adults (Carrier, 1983; Peters, 1983; Young, 2005; Fellmann, 2011) and/or behavioral adjustment of joint postures that reduce limb joint loading (Young, 2009a). Such compensatory mechanisms are considered to be a product of natural selection acting in response to differential juvenile survival (Carrier, 1996).

It is clear from the above that an ontogenetic perspective on locomotion must be incorporated into any comprehensive view of a species' ability to navigate its habitat. This may be particularly true with regard to arboreal habitats, where substrate navigation is complex, locomotor stability is at a premium, and selection pressures on juveniles might be enhanced (Lawler, 2006; Young et al., 2010). Previous biomechanical studies of locomotor ontogeny have documented heightened, even adult-like, levels of performance in a host of juvenile animals, including crickets (Dangles et al., 2007), fish (Hale, 1996; Gibb et al., 2006), birds (Dial and Jackson, 2011), salamanders (D'Aout and Aerts, 1999; Landberg and Azizi, 2010), lizards (Irschick, 2000; Toro et al., 2003), frogs (Emerson, 1978), guinea pigs (Trillmich et al., 2003), jackrabbits (Carrier, 1995), horses (Grossi and Canals, 2010), gnu (Pennycuick, 1975) and elephants (Hutchinson et al., 2006). Such studies have generally focused on acceleration, sprint speed and jumping distance, aspects of locomotor performance thought to be crucial for escaping predators and promoting juvenile survival. However, few studies have examined locomotor ontogeny in an environment where the natural diversity of substrates is represented. Field and especially lab-based studies of arboreal mammals have identified detailed kinematic or kinetic locomotor adjustments to substrate variation in adults (McClearn, 1992; Vilensky et al., 1994; Lemelin et al., 2003; Schmitt, 2003a; Schmitt and Hanna, 2004; Delciellos and Vieira, 2006; Stevens, 2006; Scheibe et al., 2007; Stevens, 2007; Nyakatura et al., 2008; Carlson and Demes, 2010; Nyakatura and Heymann, 2010; Schmidt and Fischer, 2010) but much less extensively from an ontogenetic perspective (but see Young, 2009a; Young, 2009b). In contrast, naturalistic studies of locomotor ontogeny in arboreal taxa (mainly primates) have mostly focused on ontogenetic shifts in locomotor and substrate preferences (e.g. Doran, 1992; Wells and Turnquist, 2001; Workman and Covert, 2005; Bezanson, 2009), but have provided fewer data on the specific biomechanical means by which juveniles compensate for their anatomical limitations on any particular substrate.

In a recent lab-based analysis (Shapiro and Young, 2010), we investigated kinematic responses to substrate size and orientation in adult sugar gliders (*Petaurus breviceps*, Waterhouse 1838). Sugar gliders are small-bodied, arboreal, gliding marsupials, with an average body mass of 100–160 g. In addition to gliding and vertical climbing/clinging on large trunks during exudate feeding, sugar gliders use agile quadrupedalism on substrates of mixed size and orientation (branches, flower stems) (Smith, 1982; Howard, 1989; Goldingay et al., 1991; Carthew, 1994; van Tets and Whelan, 1997). Morphological features consistent with fine-branch locomotion in *P. breviceps* include grasping hands and feet marked by a clawless, opposable hallux, reduced claw size compared with those of larger petaurids (Rasmussen and Sussman, 2007) and primate-like intrinsic hand proportions (Kirk et al., 2008).

We found that adult *P. breviceps* adjusted their quadrupedal gait (i.e. limb phase) in response to substrate type (flat board *vs* poles of three diameters) and increased limb contact time (i.e. duty factor) on the smallest diameter (0.5 cm) pole (and flat board), but did not significantly adjust limb phase in response to decreasing pole diameter. On the whole, this species was quite adept at navigating substrates of varying sizes and orientations using a lateral sequence gait, suggesting that the widespread view that a primate-like diagonal sequence gait is necessary for stable navigation of a small branch niche (e.g. Cartmill, 1972; Larson, 1998; Cartmill et al., 2002; Lemelin et al., 2003) may not pertain at small body sizes. That is, because stability on a narrow branch is inversely related to body size (Napier, 1967; Cartmill, 1985), small and large arboreal mammals may differ in biomechanical responses to a given branch diameter (Jenkins, 1974). This concept also applies to juveniles and adults because they differ in body size, but reduced body size in juveniles is compounded by their anatomical and physiological limitations discussed above. Therefore, it is important to try to distinguish whether kinematic differences between juveniles and adults are related to body size, immature musculoskeletal development, or a combination of both.

As an expansion of our previous study on adults, here we examined the ontogeny of quadrupedalism in sugar gliders, examining limb phase, duty factor and speed as before, while incorporating additional kinematic variables (hindlimb stride length, hindlimb stride frequency and hindlimb flexion at the knee). We hypothesized that the locomotion of juveniles would differ from that of adults moving across a variety of substrate diameters. Juveniles are absolutely smaller than adults and thus are smaller relative to any given substrate diameter compared with adults. Therefore, kinematic differences exhibited by juveniles and adults on a given substrate could be due to differences in body size relative to substrate size, to differences in neuromuscular development, or to both. Therefore, we tested simultaneously for the influences of relative body size and developmental status (age) on quadrupedal kinematics in sugar gliders. We asked two main questions. First, how are quadrupedal kinematics in sugar gliders affected by increases in body size relative to substrate size? We hypothesized that (regardless of age), movement across relatively smaller substrates would be associated with kinematic mechanisms that enhance stability. Second, do juveniles differ kinematically from adults in ways that enhance stability? According to the dynamic similarity hypothesis (Alexander and Jayes, 1983), geometrically similar animals traveling at the same dimensionless speeds (i.e. Froude numbers) will exhibit similar values of dimensionless kinematic variables. Therefore, kinematic differences exhibited by juveniles and adults moving at the same Froude number and at the same relative body to substrate size (i.e. lack of dynamic similarity) would support the conclusion that juveniles use distinctive kinematics to compensate for their differences in body proportions and/or immature neuromuscular development.

## MATERIALS AND METHODS

Subjects (Table 1) included three juvenile sugar gliders (*P. breviceps*) sampled longitudinally after their emergence from the pouch. *Petaurus breviceps* are born after 16 weeks gestation, weighing 0.19 g. They remain completely in the pouch until day 60, when their hindlimbs protrude. By day 70, they stop feeding from the pouch, their eyes open at day 80, and at 110–120 days (i.e. 40–50 days post-pouch) they are weaned, leave the nest and being to forage with their mother (Smith, 1973; Smith, 1979; Lindenmayer, 2002). They reach adult size at 200 days from birth, and sexual maturity at about 240 days (Smith, 1979; Lindenmayer, 2002). Body masses and kinematic data were collected every 1–2 weeks between the post-pouch ages of 28 and 80 days for two of the individuals (siblings, one male, one female) and between the post-pouch ages of 33 and 110 days for the third individual (male). Therefore, we sampled juvenile sugar gliders beginning just before the time when they would be leaving the nest in their natural habitat, and presumably encountering similar substrates to adults. The maximum age of our juveniles (110 days post-pouch) is about 20 days short of the age at which adult size is reached. For all analyses, developmental age was quantified in number of months post-emergence from the pouch. Data on juveniles were compared with those of four reproductively mature sugar gliders (two males, two females), sampled between the post-pouch ages of 6 and 11.6 months (see Shapiro and Young, 2010).

Table 1. Composition of the *Petaurus breviceps* sample

| | Age | *N* individuals | *N* strides | Body mass (g) |
|---|---|---|---|---|
| Juveniles | 0.9–2.7 months (28–80 days) | 2 | 121 | 33–62 |
| | 1.1–3.7 months (33–110 days) | 1 | 133 | 40–75 |
| Adults | 6.3–11.6 months (189–348 days) | 4 | 174 | 76–97 |

Age is given post-emergence from pouch.

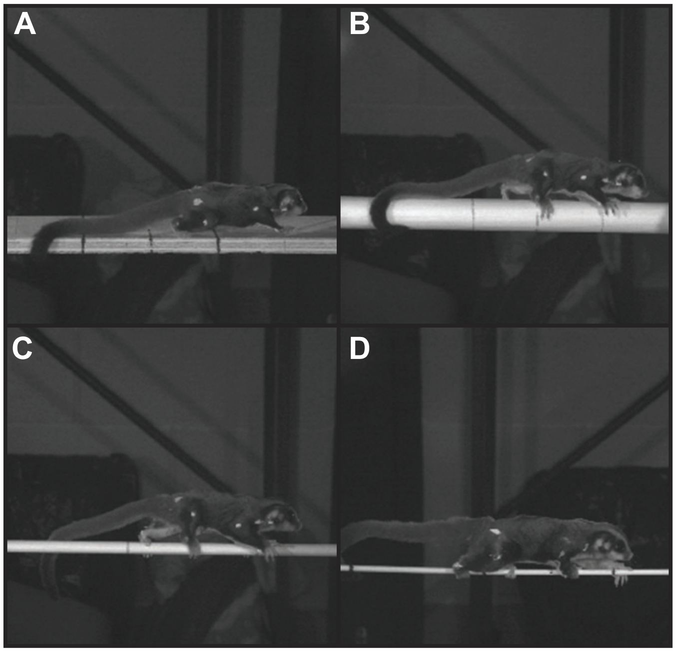

Fig. 1. Video images of a juvenile *Petaurus breviceps* (age 1.4 months post-emergence from pouch, body mass 45 g) walking on the flat board (A), the 2.5 cm pole (B), the 1 cm pole (C) and the 0.5 cm pole (D).

Subjects were filmed with five Basler 602f monochrome cameras (Basler Vision Technologies, Ahrensburg, Germany) at 100 Hz as they moved across a flat horizontal wooden board (10 cm wide) and on horizontal wooden poles of 2.5, 1.0 and 0.5 cm diameter (Fig. 1). Each substrate was 122 cm long. In order to compare individuals of different body size moving across different sized substrates, we calculated body size relative to substrate size as the cube root of body mass divided by substrate diameter. This value, hereafter referred to as 'relative body size' reflects the influence of substrate size on locomotion among both juveniles and adults. A total sample of 428 strides (254 for juveniles, 174 for adults) was analyzed across all substrate combinations. Before filming, the skin over the hip, knee, ankle, shoulder, elbow and wrist was shaved and marked with reflective tape or dots of non-toxic white paint. When necessary, animals were sedated with isoflurane anesthesia before markers were applied. Only symmetrical walks and runs were evaluated. In a perfectly symmetrical walk or run, a limb contacts the ground at exactly 50% of the time interval between footfalls of the contralateral limb (Hildebrand, 1966). Because perfect symmetry is rare, we accepted strides in which the average forelimb–hindlimb symmetry value was between 43.75% and 56.25% (Hildebrand, 1976). All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Texas at Austin.

The locomotor parameters assessed in this study include speed, limb phase, duty factor, mean limb support number, hindlimb stride length, hindlimb stride frequency and hindlimb flexion (knee joint angle). 3D coordinates of all joint markers were generated using Peak Motus (v. 9.2) software (Vicon Motion Systems, Oxford, UK), and kinematic variables were calculated using customized MATLAB routines (MathWorks, Natick, MA, USA). In order to compare aspects of locomotor behavior across individuals of different age/body size, speed, hindlimb stride length and hindlimb stride frequency were made dimensionless, as described below. Limb phase, duty factor, mean support number and knee joint angle are non-dimensional and were not converted. Although hip height (distance from the substrate surface to the hip) is conventionally used to correct for body size when testing for dynamic similarity (Alexander and Jayes, 1983; Alexander and Maloiy, 1984; Hof, 1996), given the variation in substrates in our study, we used the cube root of body mass in lieu of hip height. Hip height can be expected to change in response to changes in substrate diameter (e.g. through limb flexion), confounding the use of this variable as a proxy for body size when testing for the effects of substrate diameter. We also chose cube root of body mass in lieu of hip height because hindlimb length did not exhibit geometric similarity in our sample (Steudel-Numbers and Weaver, 2006; Schmidt, 2008).

## Kinematic variables

### Froude number, relative hindlimb stride length and relative hindlimb stride frequency

Speed was defined as the product of average stride length and average stride frequency, using values for all four limbs, where stride length is the distance traveled by a hip or shoulder marker between successive limb touchdowns, and stride frequency is the reciprocal of the time elapsed between successive limb touchdowns. In some cases, when a hip or shoulder marker was not visible, the displacement of the tip of the nose was used to calculate speed, using the pattern tracking feature in Peak Motus. Speed was made dimensionless by converting it into Froude number using the equation $u/\sqrt{(\boldsymbol{g}m)}$ [where $u$ is speed, $\boldsymbol{g}$ is gravitational acceleration ($9.81\,\mathrm{m\,s^{-2}}$) and $m$ is the cube root of body mass], hindlimb stride length was converted into relative hindlimb stride length by dividing it by the cube root of body mass, and hindlimb stride frequency was converted into relative hindlimb stride frequency by dividing it by the square root of the quotient of gravitational acceleration and the cube root of body mass (see Hof, 1996).

### Limb phase

Limb phase was defined as the proportion of stride duration that forelimb touchdown follows ipsilateral hindlimb touchdown. Divisions between named gaits are a slight modification of the divisions described by Hildebrand (Hildebrand, 1966; Hildebrand, 1976) and follow those of Cartmill et al. (Cartmill et al., 2002). Specifically, limb phase values between 0.00 and 0.25 are designated as lateral sequence, lateral couplets (LSLC) gaits, values between 0.25 and 0.50 are lateral sequence, diagonal couplets (LSDC) gaits, values between 0.50 and 0.75 are diagonal sequence, diagonal couplets (DSDC) gaits, and values between 0.75 and 1.00 are diagonal sequence, lateral couplets (DSLC) gaits. A value of 0.50 represents a trot, values of 0.00 or 1.00 represent a pace, and values of 0.25 and 0.75 represent lateral sequence and diagonal sequence single foot gaits, respectively.

### Duty factor

Duty factor was defined as the proportion of stride duration that a limb is in contact with the substrate. Rather than report duty factor for a single limb or pair of limbs, we report the mean duty factor across all four limbs as an index of the overall response to substrate type and size.

### Limb support combinations (mean support number)

Limb phase, in conjunction with duty factor, was used to calculate the relative time spent with various limb support combinations (i.e. percentage of stride duration spent on one, two, three and four limbs). Strides were resampled into 100 equally spaced intervals and measured values of limb phase, forelimb duty factor and hindlimb duty factor were used to calculate the number of contacting limbs during each interval. Values were then summed across the stride to calculate the percentage of stride duration spent on various limb combinations. Support on ipsilateral forelimbs and hindlimbs (i.e. unilateral bipedality) was scored separately from support on contralateral forelimbs and hindlimbs (i.e. diagonal bipedality) (see Cartmill et al., 2002). We then calculated the mean support number as: percentage single limb support + 2×percentage unilateral double limb support + 2×percentage diagonal double limb support + 3×percentage triple limb support + 4×percentage quadruple limb support. Mean support number can theoretically vary between 0 (no limbs in support at any time) and 4 (standing in place). Higher values indicate more limbs on the support at any one instance during the stride, theoretically conferring greater stability.

#### Hindlimb flexion (knee joint angle)

Knee joint angle was defined as the 3D vector angle between the thigh (hip to knee marker) and leg (knee to ankle marker) segments, where lower values signify more flexed hindlimbs. Knee angle data are based on a reduced sample size of 135 strides (104 for juveniles, 31 for adults). Because the knee appeared to be highly flexed throughout the stride, rather than restricting our analysis to one stride event (e.g. midstance), we averaged knee joint angle across the stance phase of the hindlimb (between touchdown and lift-off). This captures variation in knee flexion and avoids the assumption that flexion is deepest at any one given point in the stride.

### Functional rationale and predictions for kinematic variables

#### Functional rationale for limb phase

Primates and some arboreal to semi-arboreal marsupials (e.g. *Caluromys*, *Dromiciops*, *Trichosurus*) share a preference for limb phases that correspond to DSDC walking gaits (Hildebrand, 1967; White, 1990; Pridmore, 1994; Lemelin et al., 2003; Reilly et al., 2010) [but see Shapiro and Young (Shapiro and Young, 2010) for discussion of *Dromiciops*]. DSDC walking, along with a complex of other kinematic features, has been associated with adaptation to a small branch arboreal niche (Larson, 1998; Cartmill et al., 2002; Lemelin et al., 2003; Cartmill et al., 2007), but the potential biomechanical advantage provided by DSDC for walking on small diameter substrates remains unclear (Stevens, 2006; Shapiro and Raichlen, 2007; Stevens, 2007; Wallace and Demes, 2008), and adult sugar gliders prefer LSDC walking, even on very narrow substrates (Shapiro and Young, 2010). In addition, infant primates have been shown to differ from adults in their gait preferences as a means to enhance stability or reduce limb interference (Hildebrand, 1967; Rose, 1977; Rollinson and Martin, 1981; Hurov, 1982; Vilensky and Gankiewicz, 1989; Nakano, 1996; Dunbar and Badam, 1998; Shapiro and Raichlen, 2005; Shapiro and Raichlen, 2006). Ontogenetic transitions in limb phase have also been documented for other mammals such as cats (Peters, 1983) and rodents (Eilam, 1997). Nevertheless, no study has addressed the impact of ontogenetic gait transitions on arboreal navigation specifically, and the ontogeny of limb phase in marsupials moving on arboreal substrates is, to our knowledge, unknown. In this study, the functional effect of limb phase (i.e. contribution to stability on a substrate) was assessed by calculating mean limb support number using limb phase and duty factor values during a given stride.

#### Prediction for effect of relative body size on limb phase

In our previous study on adult sugar gliders, we found that limb phase increased on poles compared with a flat board, but decreases in pole diameter (i.e. increases in relative body size) were not accompanied by significant adjustments in limb phase. Therefore, we expected similar results when juveniles were added to the sample and differences due to age were controlled for, i.e. a significant effect of relative body size on limb phase when moving from board to poles, but no significant effect of relative body size on limb phase across poles of different diameter.

#### Prediction for effect of age on limb phase

Younger juveniles were predicted to differ from older juveniles and adults with respect to preferred limb phase values, and were predicted to use limb phase/duty factor combinations that enhance stability in comparison to older juveniles or adults at a given relative body to substrate size.

#### Functional rationale for duty factor

Duty factor is inversely related to speed (Hildebrand, 1976), but at a given speed, higher duty factors are presumed to confer enhanced stability by prolonging limb contact time (Schmitt, 1999; Stevens, 2003; Shapiro et al., 2011).

#### Prediction for effect of relative body size on duty factor

In our previous study on adult sugar gliders (Shapiro and Young, 2010), duty factor (at a given speed) was highest on both the smallest diameter (0.5 cm) pole and the flat board. Increased duty factor on the smallest pole likely reflected the need for increased stability at relatively large body size to substrate size. Increased duty factor on the flat board may be associated with the fact that a broad, flat surface is a relatively unnatural substrate for a highly arboreal mammal. Here, we predicted similar results; that after controlling for age, duty factor (across poles) would increase as relative body size increases, but that duty factor would also be increased on the flat board.

#### Prediction for effect of age on duty factor

At a given relative body to substrate size, younger juveniles were predicted to use higher duty factors than older juveniles or adults at a given relative body to substrate size to enhance stability.

#### Functional rationale for mean support number

It was assumed that stability increases with the number of limbs in support, and that in two-limbed support, support by diagonal limbs provides greater stability than support by ipsilateral limbs (Vilensky and Gankiewicz, 1989; Cartmill et al., 2002). That is, grasping diagonal limbs generate opposing torques that promote mediolateral stability on an arboreal substrate (Prost, 1969; Crompton et al., 2000; Li, 2000; Preuschoft, 2002; Schmidt, 2005; Cartmill et al., 2007; Schmidt, 2008; Young and Demes, 2010).

#### Prediction for effect of relative body size on mean support number

At a given age, mean support number was predicted to increase as relative body to substrate size increased.

#### Prediction for effect of age on mean support number

Younger juveniles were predicted to use higher mean support numbers than older juveniles or adults at a given relative body size, as a means to enhance stability.

#### Functional rationale for relative hindlimb stride length and stride frequency

In an arboreal context, long strides and low stride frequencies at a given speed have been considered to be part of a complex of features associated with 'compliant' gait, which benefits arboreal locomotion

Table 2. Summary statistics for juveniles and adults on all substrates and poles alone

| | | Juveniles | Adults |
|---|---|---|---|
| Total *N* | All substrates | 254 | 174 |
| | Poles alone | 183 | 131 |
| Froude number | All substrates | 0.297±0.13 (0.097–0.949) | 0.349±0.24 (0.094–1.820) |
| | Poles alone | 0.292±0.14 (0.097–0.949) | 0.357±0.26 (0.094–1.820) |
| Limb phase | All substrates | 0.361±0.10 (0.118–0.598) | 0.454±0.07 (0.251–0.645) |
| | Poles alone | 0.368±0.10 (0.118–0.598) | 0.474±0.07 (0.260–0.645) |
| Duty factor | All substrates | 0.661±0.08 (0.510–0.882) | 0.612±0.06 (0.412–0.766) |
| | Poles alone | 0.652±0.07 (0.510–0.851) | 0.607±0.06 (0.412–0.753) |
| Mean limb support | All substrates | 2.635±0.31 (2.020–3.520) | 2.440±0.23 (1.640–3.060) |
| | Poles alone | 2.598±0.29 (2.020–3.400) | 2.416±0.23 (1.640–3.000) |
| Relative stride length | All substrates | 2.220±0.54 (0.769–4.284) | 2.319±0.38 (1.498–4.396) |
| | Poles alone | 2.256±0.55 (0.769–4.284) | 2.339±0.41 (1.498–4.396) |
| Relative stride frequency | All substrates | 0.129±0.03 (0.0522–0.265) | 0.156±0.08 (0.0501–0.447) |
| | Poles alone | 0.127±0.03 (0.0522–0.265) | 0.155±0.08 (0.0501–0.447) |
| Mean knee joint angle during stance phase | All substrates | 67.247±8.297 (43.562–105.274) | 93.642±9.286 (67.567–108.502) |
| | Poles alone | 68.024±8.607 (54.635–105.274) | 94.887±9.468 (67.567–108.502) |

For each dependent variable, mean ± s.d. values are presented, with ranges in parentheses.

and enhances stability by reducing substrate reaction forces on limbs and minimizing branch oscillations (Demes et al., 1990; Schmitt, 1999). In primates, these kinematic features may have evolved as a by-product of the distally distributed limb mass associated with grasping musculature (Preuschoft and Günther, 1994; Raichlen, 2004). Moreover, because of enhanced grasping musculature for clinging to their mothers, muscle mass is more distally distributed, strides are relatively longer, and stride frequencies are relatively lower in infant primates compared with adults (Raichlen, 2005a; Raichlen, 2005b).

### Prediction for effect of relative body size on relative hindlimb stride length and stride frequency

If long strides and low stride frequencies function to enhance stability on small branches, reduce branch oscillations, and reduce limb loading, we predicted that at any given age, stride length would increase and stride frequency would decrease as body size relative to substrate size increased (i.e. as relative substrate diameter decreased).

### Prediction for effect of age on relative hindlimb stride length and stride frequency

We do not have data on the limb inertial properties of the limbs in sugar gliders. Therefore we cannot test whether juveniles differ from adults in relative stride length or frequency as a by-product of enhanced grasping musculature as in primates (Raichlen, 2005a; Raichlen, 2005b). Once out of the pouch, sugar gliders will ‘ride’ on the back of their mother or father, but this is an intermittent activity, and they are often left in the nest while the parents forage (Smith, 1971; Holloway and Geiser, 2000). By contrast, most primates cling fairly continuously to their mothers until they reach locomotor independence (Altmann, 2001; Ross, 2001). Therefore, we cannot discern whether any variation in stride characteristics between juveniles and adults is a byproduct of limb mass distribution or rather a means of directly enhancing stability to compensate for relatively weak muscles and immature neuromotor coordination. Regardless, we predicted that younger juveniles would use relatively longer strides and lower stride frequencies than older juveniles or adults.

### Functional rationale for hindlimb flexion

In an arboreal context, increased limb flexion enhances stability by bringing the body’s center of mass closer to the substrate, minimizing the risk of toppling (Napier, 1967; Rose, 1974; Cartmill, 1985; Preuschoft et al., 1995; Schmitt, 1999; Stevens, 2003).

### Prediction for effect of relative size on hindlimb flexion

We predicted that at a given age, hindlimb flexion would increase as body size relative to substrate size increased.

### Prediction for effect of age on hindlimb flexion

We predicted that younger juveniles would use more flexed hindlimb postures than older juveniles or adults because of immature muscular development and/or in order to enhance stability at a given relative body to substrate size. More flexed hindlimbs at younger ages regardless of substrate (i.e. relative body size) would suggest that the age-related flexion is due to relatively weak anti-gravity limb musculature. More flexed hindlimb postures at younger ages on the poles but not on the flat board would suggest that the age-related difference is due to the need for stability, but weak musculature could nonetheless be a contributing factor.

## Statistical analyses

Summary statistics for all variables are presented in Table 2. In addition, we employed multiple regression to test for the relative effects of three independent variables on each kinematic variable: age, relative body (to substrate) size and (because there is ample evidence that speed influences many aspects of locomotor kinematics) Froude number. Because it is conventional to regress limb phase against duty factor, and duty factor has been shown to be correlated with limb phase (Cartmill et al., 2002; Lemelin et al., 2003; Hutchinson et al., 2006; Young et al., 2007; McElroy, 2008; Young, 2008), we also included duty factor as a fourth independent variable in the multiple regression for limb phase. Froude number has no significant effect on limb phase once duty factor is controlled for. Therefore, we reran the multiple regression on limb phase using only duty factor, age and relative body size as independent variables. All multiple regressions were first run across the entire age sample (juveniles and adults combined), and then on the juvenile sample separately. This allowed us to interpret whether differences that distinguish juveniles from adults also characterize juveniles of different ages. When significant effects were found in the full juvenile/adult sample but not within juveniles alone, we concluded that significance was driven by juveniles as a group *vs* adults. Similarly, we ran multiple regressions on all substrates combined (flat board plus three poles) and then on poles alone in order to distinguish effects due to differences in substrate type from those due to substrate size. When significant effects were found in the full substrate sample but not for

Table 3. Multiple regression models testing the effects of duty factor, relative body size and age on limb phase in *P. breviceps*

| Regression model | *N* | Intercept | Regression coefficient | Standard error | *P*-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| All ages, all substrates | 428 | 1.043 | | | | 0.734 |
| Duty factor | | | –1.052 | 0.0371 | <0.001 | |
| Relative size | | | 0.000217 | 0.0000895 | 0.016 | |
| Age | | | 0.00485 | 0.000756 | <0.001 | |
| All ages, poles only | 314 | 1.082 | | | | 0.742 |
| Duty factor | | | –1.120 | 0.0484 | <0.001 | |
| Relative size | | | 0.000134 | 0.000123 | 0.277 | |
| Age | | | 0.00668 | 0.000932 | <0.001 | |
| Juveniles, all substrates | 254 | 1.088 | | | | 0.762 |
| Duty factor | | | –1.106 | 0.0476 | <0.001 | |
| Relative size | | | –0.000189 | 0.000113 | 0.097 | |
| Age | | | 0.0048 | 0.00492 | 0.325 | |
| Juveniles, poles only | 183 | 1.170 | | | | 0.761 |
| Duty factor | | | –1.247 | 0.0629 | <0.001 | |
| Relative size | | | –0.0000132 | 0.000161 | 0.934 | |
| Age | | | 0.00529 | 0.00625 | 0.399 | |

poles alone, we concluded that significance was driven by substrate type. For all analyses, the significance level was set to $P<0.05$.

## RESULTS

### Limb phase

#### Effect of duty factor on limb phase

Duty factor had a significantly inverse relationship with limb phase in all comparisons, when controlling for variation in age and relative body size (Table 3).

#### Effect of relative body size on limb phase

After controlling for duty factor and age, the effect of relative size on limb phase reached significance only for the combined substrate/age sample (Table 3). That is, among juveniles and adults combined moving across all substrates, limb phase increased significantly as relative body to substrate size increased (Table 3, Fig. 2A). Among juveniles alone moving across all substrates, there was a similar trend that did not reach statistical significance ($P$=0.097). When the flat board was excluded from the sample, there was no significant effect of relative size either for the combined age sample (Table 3, Fig. 2B) or for juveniles only (Table 3).

#### Effect of age on limb phase

After controlling for duty factor and relative size, younger sugar gliders used lower limb phases than older gliders, across all substrates combined (flat board and poles; Table 3, Fig. 2C) as well as among poles alone (Table 3, Fig. 2D). In other words, even when moving with similar duty factors at the same relative body size to pole diameter, younger sugar gliders use lower limb phases than older sugar gliders. The age-related differences in limb phase thus appear to be associated with the challenges of juvenility rather than a simple effect of being smaller or larger relative to the substrate. This age effect appears to be a juvenile *vs* adult difference, as there was no significant age effect when juveniles were considered separately (Table 3). When limb phases were associated with named gaits, both juveniles and adults used LSDC gaits on average, but the range used by juveniles extended into LSLC (Table 2, Fig. 2E).

### Duty factor

#### Effect of Froude number on duty factor

For all comparisons discussed below, Froude number had a significant inverse relationship with duty factor, even after controlling for age and relative body to substrate size (Table 4). This was expected, as it is well known that duty factor and speed are inversely correlated (e.g. Hildebrand, 1976).

#### Effect of relative body size on duty factor

As predicted, when the effects of Froude number and age were controlled for, relative body size influenced duty factor. Across all

Table 4. Multiple regression models testing the effects of log Froude number, relative body size and age on log duty factor in *P. breviceps*

| Regression model | *N* | Intercept | Regression coefficient | Standard error | *P*-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| All ages, all substrates | 316 | –0.264 | | | | 0.598 |
| log Froude number | | | –0.148 | 0.00797 | <0.001 | |
| Relative size | | | 0.000101 | 0.0000569 | 0.075 | |
| Age | | | –0.00335 | 0.000427 | <0.001 | |
| All ages, poles only | 232 | –0.283 | | | | 0.670 |
| log Froude number | | | –0.141 | 0.00817 | <0.001 | |
| Relative size | | | 0.000531 | 0.0000679 | <0.001 | |
| Age | | | –0.00393 | 0.000454 | <0.001 | |
| Juveniles, all substrates | 207 | –0.269 | | | | 0.633 |
| log Froude number | | | –0.168 | 0.0112 | <0.001 | |
| Relative size | | | 0.000104 | 0.0000686 | 0.131 | |
| Age | | | –0.00720 | 0.00312 | 0.022 | |
| Juveniles, poles only | 148 | –0.284 | | | | 0.687 |
| log Froude number | | | –0.161 | 0.0118 | <0.001 | |
| Relative size | | | 0.000497 | 0.0000811 | <0.001 | |
| Age | | | –0.00898 | 0.00349 | 0.011 | |

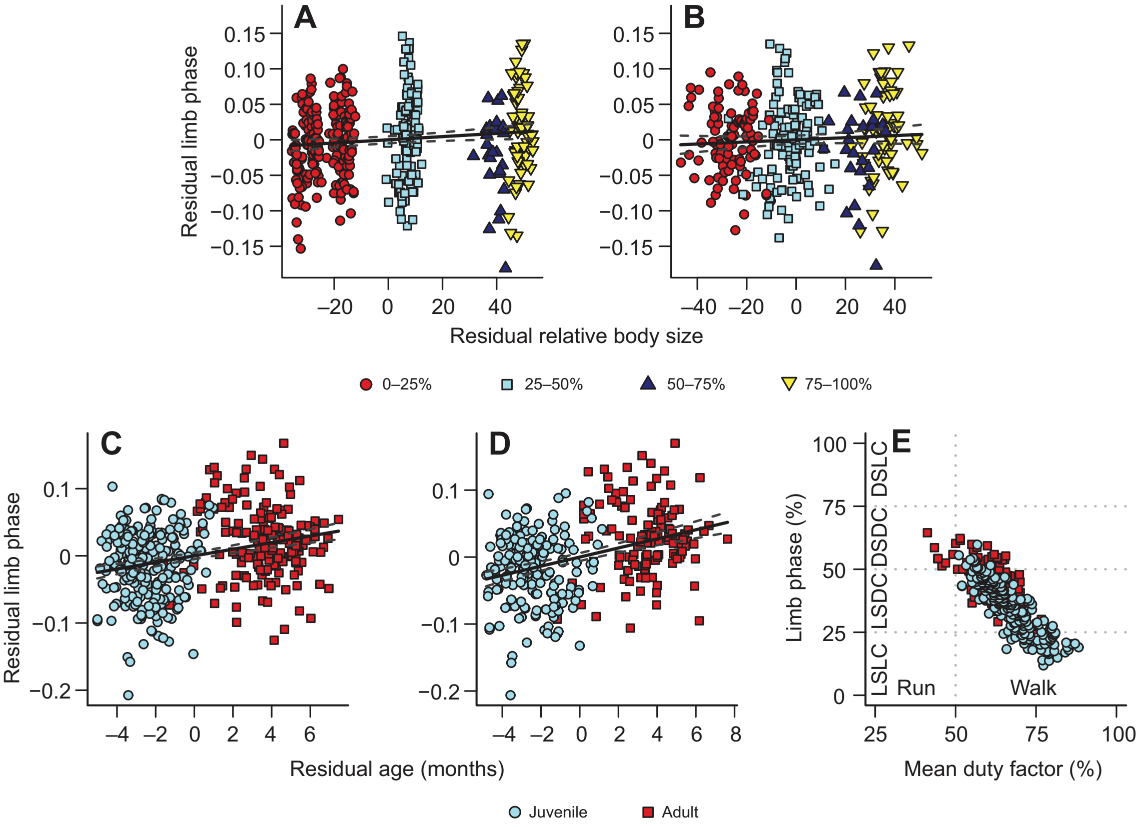

Fig. 2. Effects of relative body size and developmental age on limb phase in *P. breviceps*. A–D illustrate the results of multiple regressions of limb phase modeled as a function of relative body size, age in months and mean duty factor. The multiple regression analysis was performed on continuous data, but for visual reference, data points were grouped into four percentage categories representing relative body size (see Materials and methods) and two age categories. (A) Partial regression plot of limb phase *vs* relative body size for locomotion across all substrates, controlling for age in months and mean duty factor. (B) Partial regression plot of limb phase *vs* relative body size for locomotion on the poles alone, controlling for age in months and mean duty factor. (C) Partial regression plot of limb phase *vs* age in months for locomotion across all substrates, controlling for relative body size and mean duty factor. (D) Partial regression plot of limb phase *vs* age in months for locomotion on poles alone, controlling for relative body size and mean duty factor. (E) Gait graph (Hildebrand, 1966) of limb phase *vs* mean duty factor in juvenile and adult *P. breviceps*. The divisions between discrete gaits, categorized according to limb phase, and between walks and runs, categorized according to mean duty factor, are indicated on the plot. LSLC, lateral sequence, lateral couplets gait; LSDC, lateral sequence, diagonal couplets gait; DSDC, diagonal sequence, diagonal couplets gait; DSLC, diagonal sequence, lateral couplets gait.

ages, or within juveniles alone, duty factor increased with relative body to substrate size, but only when the poles were considered separately (Table 4, Fig. 3B). As in our previous study on adults (Shapiro and Young, 2010), the use of relatively high duty factors on the largest (flat board) and smallest substrate (0.5 cm pole) most likely accounts for the lack of a relative size effect when the board and poles are considered together (Table 4, Fig. 3A).

### Effect of age on duty factor

As predicted, when the effects of Froude number and relative size were controlled for, younger gliders used significantly higher duty factors than older gliders. This holds across all substrates (flat board and poles; Table 4, Fig. 3C) and for poles alone (Table 4, Fig. 3D). The significant effect of age applies to the combined age sample as well as within juveniles (Table 4).

## Mean limb support

### Effect of Froude number on mean limb support

For all comparisons discussed below, Froude number had a significant inverse relationship with mean limb support, even after controlling for age and relative body size (Table 5). That is, faster speeds were associated with reduced overall limb support.

### Effects of relative body size on mean limb support

As predicted, across all ages, or within juveniles alone, mean limb support increased with relative body to substrate size, but only when poles were considered separately (Table 5, Fig. 4B). Because the calculation of mean limb support is based in large part on duty factor values, these results resemble those reported for duty factor. That is, relatively high duty factors on the largest (flat board) and smallest substrate (0.5 cm pole) lead to high values of mean limb support at the lowest and highest relative body sizes, which in turn would mask the relative body size effect when boards and poles are considered together (Table 5, Fig. 4A).

### Effect of age on mean limb support

As predicted, when the effects of Froude number and relative size were controlled for, younger gliders were supported by more limbs on average during a stride than were older gliders. This holds across all substrates (flat board and poles; Table 5, Fig. 4C) and for poles alone (Table 5, Fig. 4D). The significant effect of age applies to the combined age sample as well as within juveniles. Compared with adults, juveniles employed a significantly higher percentage of triple limb support, and a significantly lower percentage of diagonal bipedality ($P<0.001$, Mann–Whitney rank sum) (Fig. 4E,F).

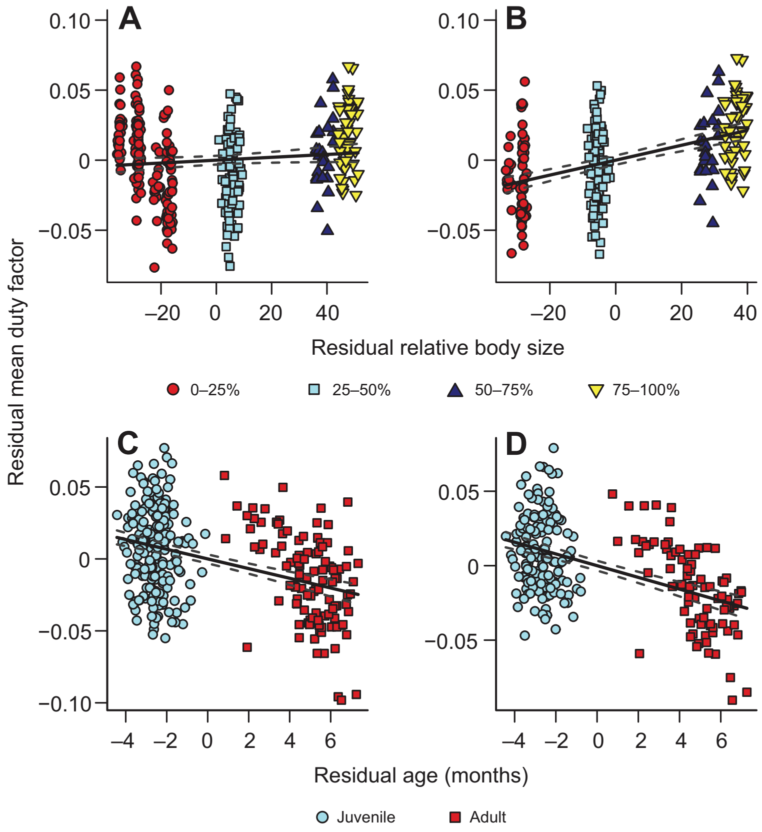

Fig. 3. Effects of relative body size and developmental age on mean duty factor in *P. breviceps*. A–D illustrate the results of multiple regressions of mean duty factor modeled as a function of relative body size, age in months and Froude number. The multiple regression analysis was performed on continuous data, but for visual reference, data points were grouped into four percentage categories representing relative body size (see Materials and methods) and two age categories. (A) Partial regression plot of mean duty factor *vs* relative body size for locomotion across all substrates, controlling for age in months and Froude number. (B) Partial regression plot of mean duty factor *vs* relative body size for locomotion on the poles alone, controlling for age in months and Froude number. (C) Partial regression plot of mean duty factor *vs* age in months for locomotion across all substrates, controlling for relative body size and Froude number. (D) Partial regression plot of mean duty factor *vs* age in months for locomotion on poles alone, controlling for relative body size and Froude number.

## Relative hindlimb stride length

### Effect of Froude number on relative stride length

For all comparisons discussed below, Froude number had a significant effect on relative stride length, even after controlling for the effects of age and relative body size. That is, relative stride length increased with relative speed.

### Effects of relative body size on relative stride length

Across all ages, on all substrates combined (Table 6, Fig. 5A), as well as on poles only (Table 6, Fig. 5B), relative body size had a significant effect on relative stride length after the effects of age and Froude number were controlled for. That is, as body size increased relative to substrate size, relative stride length increased. This effect also applied within the juvenile sample separately, but only when the board and poles were considered together. On poles alone, there was no effect of relative body size on relative stride length for juveniles (Table 6). However, given the significant effect of relative body size on poles alone for all ages, the lack of significance for poles alone within juveniles could be a statistical artifact of reduced sample sizes when age groups are considered separately.

### Effects of age on relative stride length

Across all ages, on all substrates, age had a significant effect on relative stride length, but in the opposite direction from predictions: older gliders used significantly (but not dramatically) longer strides

Table 5. Multiple regression models testing the effects of log Froude number, relative body size and age on log mean support number in *P. breviceps*

| Regression model | $N$ | Intercept | Regression coefficient | Standard error | $P$-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| All ages, all substrates | 316 | 0.336 | | | | 0.596 |
| log Froude number | | | –0.148 | 0.00802 | <0.001 | |
| Relative size | | | 0.000102 | 0.0000571 | 0.076 | |
| Age | | | –0.00340 | 0.000431 | <0.001 | |
| All ages, poles only | 232 | 0.317 | | | | 0.667 |
| log Froude number | | | –0.141 | 0.00825 | <0.001 | |
| Relative size | | | 0.000531 | 0.0000685 | <0.001 | |
| Age | | | –0.00396 | 0.000460 | <0.001 | |
| Juveniles, all substrates | 207 | 0.331 | | | | 0.630 |
| log Froude number | | | –0.169 | 0.0113 | <0.001 | |
| Relative size | | | 0.000103 | 0.0000691 | 0.136 | |
| Age | | | –0.00677 | 0.00308 | 0.029 | |
| Juveniles, poles only | 148 | 0.316 | | | | 0.683 |
| log Froude number | | | –0.161 | 0.0120 | <0.001 | |
| Relative size | | | 0.000497 | 0.0000820 | <0.001 | |
| Age | | | –0.000297 | 0.000118 | 0.013 | |

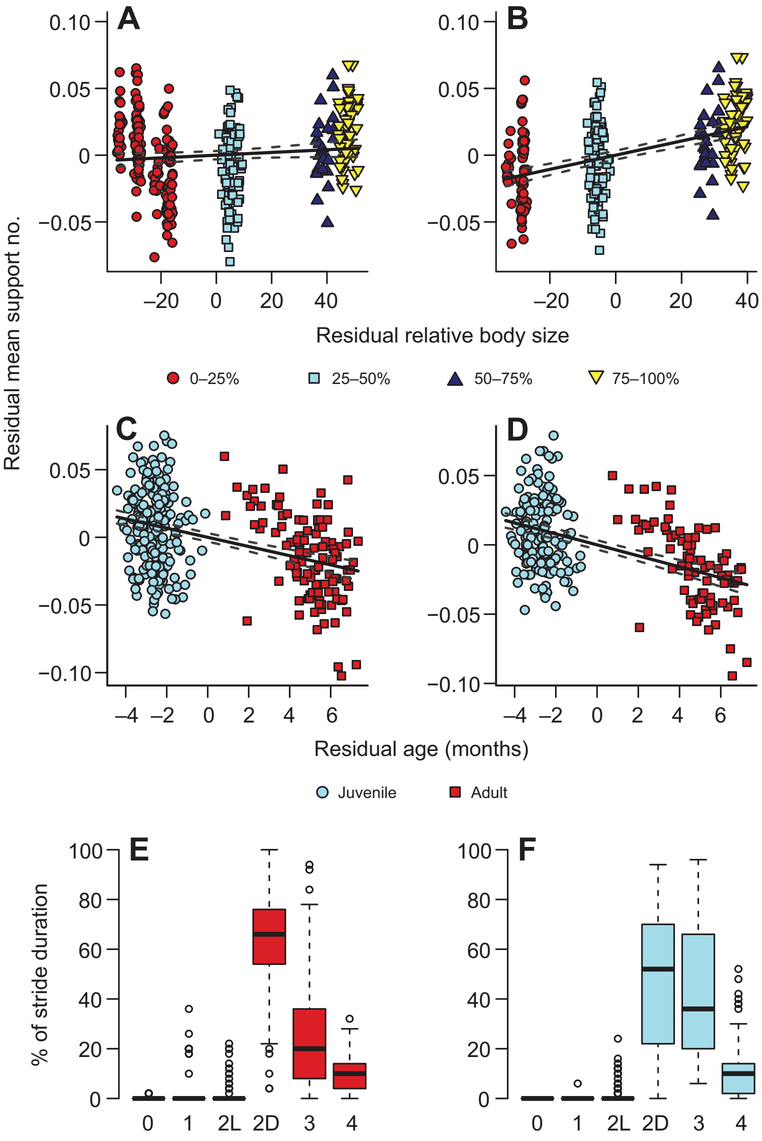

Fig. 4 Effects of relative body size and developmental age on mean support number in *P. breviceps.* A–D illustrate the results of multiple regressions of mean support number modeled as a function of relative body size, age in months and Froude number. The multiple regression analysis was performed on continuous data, but for visual reference, data points were grouped into four percentage categories representing relative body size (see Materials and methods) and two age categories. (A) Partial regression plot of mean support number *vs* relative body size for locomotion across all substrates, controlling for age in months and Froude number. (B) Partial regression plot of mean support number *vs* relative body size for locomotion on the poles alone, controlling for age in months and Froude number. (C) Partial regression plot of mean support number *vs* age in months for locomotion across all substrates, controlling for relative body size and Froude number. (D) Partial regression plot of mean support number *vs* age in months for locomotion on poles alone, controlling for relative body size and Froude number. E and F are box plots of the percentage of stride duration spent on no limbs (aerial phase), one limb, two lateral limbs (2L), two diagonal limbs (2D), three limbs and four limbs in adult (E) and juvenile (F) *P. breviceps*.

than younger gliders after relative body size and Froude number were controlled for (Table 6, Fig. 5C). However, when the flat board was excluded from the all ages sample, the age effect became non-significant (Fig. 5D). In contrast, age had a highly significant ($P<0.001$) effect on relative stride length within juveniles. Compared with younger juveniles, older juveniles used relatively longer strides at a given relative body size or Froude number, across all substrates or on poles alone (Table 6, Fig. 5E,F).

## Relative hindlimb stride frequency

### Effect of Froude number on relative stride frequency

For all comparisons discussed below, Froude number had a significantly positive relationship with relative stride frequency, even after controlling for the effects of age and relative body size (Table 7). That is, relative stride frequency increased with relative speed.

### Effect of relative body size on relative stride frequency

Across all ages, on all substrates combined (Table 7, Fig. 6A), as well as on poles only (Table 7, Fig. 6B), relative body size had a significant effect on relative stride frequency after the effects of age and Froude number were controlled for. That is, as body size increased relative to substrate size, relative stride frequency decreased. This effect also applied within the juvenile sample separately, but only when the board and poles were considered together. On poles alone, there was no effect of relative body size on relative stride frequency for juveniles.

### Effect of age on relative stride frequency

Across all ages, all substrates (Table 7, Fig. 6C), or all ages, poles only (Table 6, Fig. 6D), age had no significant effect on relative stride frequency. However, as was the case for relative stride length, age did have a significant (but inverse) effect on relative stride frequency within juveniles; older juveniles used relatively lower stride frequencies than younger juveniles, across all substrates ($P<0.001$) (Table 7, Fig. 6E), or on poles alone ($P<0.001$) (Table 7, Fig. 6F).

## Hindlimb flexion

### Effect of Froude number on hindlimb flexion

Across all ages and all substrates, Froude number had a significant inverse relationship with knee joint angle (i.e. more highly flexed limbs at higher relative speeds) (Table 8). However, for all other

Table 6. Multiple regression models testing the effects of log Froude number, relative body size and age on log relative stride length in *P. breviceps*

| Regression model | *N* | Intercept | Regression coefficient | Standard error | *P*-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| All ages, all substrates | 316 | 0.524 | | | | 0.669 |
| log Froude number | | | 0.380 | 0.0157 | <0.001 | |
| Relative size | | | 0.000477 | 0.000112 | <0.001 | |
| Age | | | 0.00171 | 0.000844 | 0.043 | |
| All ages, poles only | 232 | 0.522 | | | | 0.651 |
| log Froude number | | | 0.368 | 0.0185 | <0.001 | |
| Relative size | | | 0.000439 | 0.000153 | 0.005 | |
| Age | | | 0.00133 | 0.00103 | 0.196 | |
| Juveniles, all substrates | 207 | 0.480 | | | | 0.779 |
| log Froude number | | | 0.414 | 0.0211 | <0.001 | |
| Relative size | | | 0.000496 | 0.000129 | <0.001 | |
| Age | | | 0.0335 | 0.00588 | <0.001 | |
| Juveniles, poles only | 148 | 0.446 | | | | 0.787 |
| log Froude number | | | 0.388 | 0.0242 | <0.001 | |
| Relative size | | | 0.000269 | 0.000166 | 0.108 | |
| Age | | | 0.0487 | 0.00716 | <0.001 | |

comparisons (all ages, poles only, or comparisons within juveniles), there was no effect of Froude number on hindlimb flexion.

### Effect of relative body size on hindlimb flexion

Contrary to predictions, there was no effect of relative body size on hindlimb flexion across all ages or within juveniles, either when all substrates were considered or when poles were considered alone (Table 8, Fig. 7A,B). Interestingly, adults showed a significant tendency to walk with more extended hindlimbs on the poles relative to the flat board, although the available sample size was low (*N*=31).

### Effect of age on hindlimb flexion

As predicted, across the full age sample (all substrates as well as poles alone), age had a significant (positive) relationship with knee joint angle (i.e. younger sugar gliders have more flexed hindlimbs than older sugar gliders), but age had no effect on hindlimb flexion within the juvenile sample (Table 8, Fig. 7C,D). Therefore, the differences within the full age sample signify that juveniles use more flexed hindlimbs during stance phase at a given Froude number or at a given relative body size than adults. Multiple regression analysis on knee angle at touchdown and lift-off indicated that although juveniles used more flexed knees at lift-off than adults (across all substrates or on poles alone, *P*<0.001), the age-related difference in mean knee angle persists even when knee angle at lift-off is controlled for.

## DISCUSSION

### Substrate diameter affects quadrupedal kinematics in *P. breviceps*

Although the main goal of this study was to compare the locomotion of juvenile and adult sugar gliders across substrates of varying size, owing to their absolute differences in body size, the specific influence of juvenility (i.e. immature neuromuscular development) on any given substrate cannot be assessed without also considering the effect of relative body size to substrate size. Starting with the basic assumption that in arboreal mammals, stability is inversely related to relative body size, we hypothesized that sugar gliders would employ kinematic stabilizing mechanisms as body size increased relative to substrate diameter. Previous studies have tested for the effects of decreasing substrate diameter on quadrupedal kinematics in arboreal (Schmitt, 2003a; Delciellos and Vieira, 2006; Stevens, 2006; Delciellos and Vieira, 2007; Scheibe et al., 2007; Stevens, 2007; Lemelin and Cartmill, 2010) and non-arboreal (Lammers and Biknevicius, 2004; Lammers,

Table 7. Multiple regression models testing the effects of log Froude number, relative body size and age on log relative stride frequency in *P. breviceps*

| Regression model | *N* | Intercept | Regression coefficient | Standard error | *P*-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| All ages, all substrates | 316 | –0.535 | | | | 0.844 |
| log Froude number | | | 0.614 | 0.0151 | <0.001 | |
| Relative size | | | –0.000429 | 0.000108 | <0.001 | |
| Age | | | –0.00109 | 0.000809 | 0.180 | |
| All ages, poles only | 232 | –0.526 | | | | 0.851 |
| log Froude number | | | 0.631 | 0.0176 | <0.001 | |
| Relative size | | | –0.000428 | 0.000146 | 0.004 | |
| Age | | | –0.00105 | 0.000978 | 0.282 | |
| Juveniles, all substrates | 207 | –0.484 | | | | 0.830 |
| log Froude number | | | 0.586 | 0.0197 | <0.001 | |
| Relative size | | | –0.000385 | 0.000121 | 0.002 | |
| Age | | | –0.0358 | 0.00549 | <0.001 | |
| Juveniles, poles only | 148 | –0.457 | | | | 0.839 |
| log Froude number | | | 0.609 | 0.0229 | <0.001 | |
| Relative size | | | –0.000258 | 0.000157 | 0.103 | |
| Age | | | –0.0456 | 0.00675 | <0.001 | |

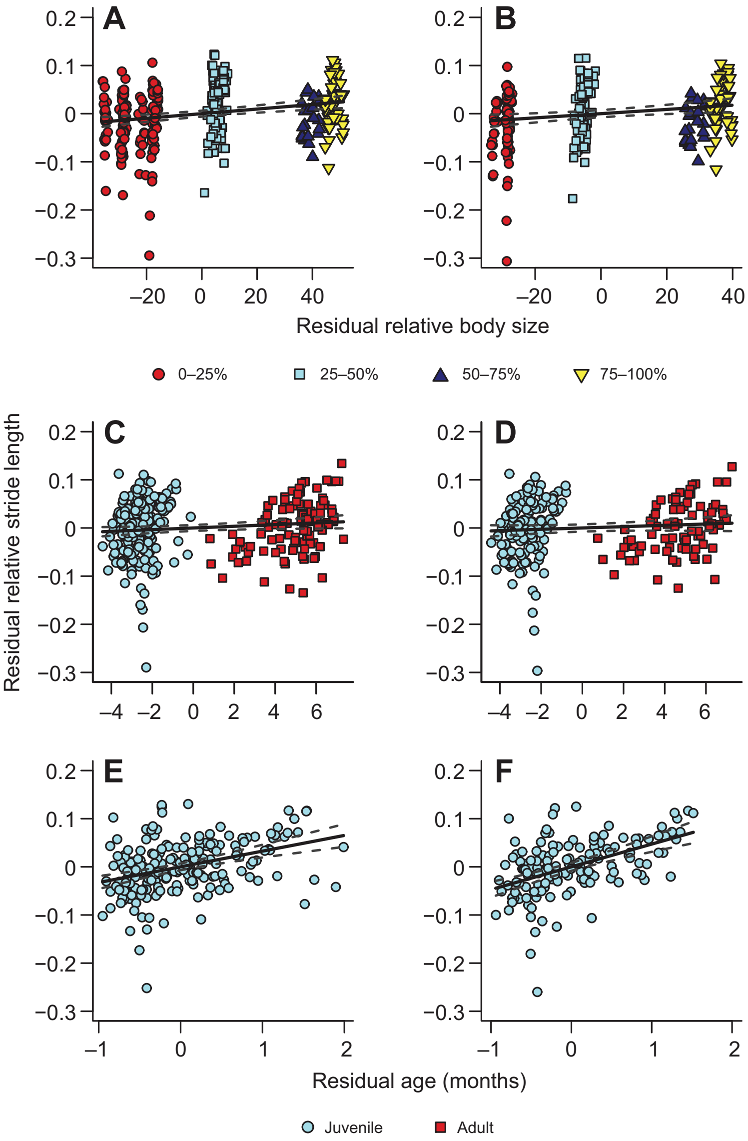

Fig. 5. Effects of relative body size and developmental age on relative hindlimb stride length in *P. breviceps*. A–F illustrate the results of multiple regressions of relative stride length modeled as a function of relative body size, age in months and Froude number. The multiple regression analysis was performed on continuous data, but for visual reference, data points were grouped into four percentage categories representing relative body size (see Materials and methods) and two age categories. (A) Partial regression plot of relative stride length *vs* relative body size for locomotion across all substrates, controlling for age in months and Froude number. (B) Partial regression plot of relative stride length *vs* relative body size for locomotion on the poles alone, controlling for age in months and Froude number. (C) Partial regression plot of relative stride length *vs* age in months for locomotion across all substrates, controlling for relative body size and Froude number. (D) Partial regression plot of relative stride length *vs* age in months for locomotion on poles alone, controlling for relative body size and Froude number. (E) Partial regression plot of relative stride length *vs* age in months for locomotion across all substrates in juveniles alone, controlling for relative body size and Froude number. (F) Partial regression plot of relative stride length *vs* age in months for locomotion on poles in juveniles alone, controlling for relative body size and Froude number.

2007; Schmidt and Fischer, 2010) mammals, but these studies have been restricted to adult subjects at a given body size. By including both adults and juveniles in our sample, and by tracking kinematics longitudinally through ontogeny, our study has the added advantage of permitting the assessment of the effects of relative body (to substrate) size on locomotion across a more extensive range of body sizes within a single species (see also Young, 2009a). Overall, our results for the effects of relative body size on quadrupedal kinematics are consistent with those of our previous study on adult sugar gliders (Shapiro and Young, 2010), but expand the variables considered, while adding the new finding that kinematic adjustments by sugar gliders to decreasing relative substrate diameter occur regardless of age.

By examining the effects of relative body to substrate size while controlling for differences in age (and relative speed), our analysis confirmed our hypothesis that sugar gliders adjust some aspects of their quadrupedal kinematics when faced with decreases in relative substrate diameter. Considering poles alone, when faced with a decrease in relative substrate diameter, sugar gliders (regardless of age) increased duty factor, increased the average number of supporting limbs used during a stride, increased relative stride length and decreased relative stride frequency (although for these last two variables, the effect within juveniles did not reach significance). A relative decrease in pole diameter had no significant effect on limb phase or on knee flexion.

When the flat board was included along with the poles in the substrate sample, flexion at the knee remained unaffected, with the exception of adults, who showed a tendency for flexion to decrease as relative body size to substrate size increased. Limb phase (which did not vary across poles of varying diameter) increased significantly with increases in relative body size (across all substrates and ages, with a similar trend among juveniles), indicating an effect of substrate type (flat *vs* cylindrical) rather than substrate diameter. The increases in relative stride length and decreases in relative stride frequency observed during locomotion on poles alone remained statistically significant. However, the significant effects of relative body size on duty factor and limb support combinations dropped out. This is most likely attributable to increases in these last two variables on the largest (board) and smallest (0.5 cm pole) substrates. Nevertheless, although specific kinematic accommodation may have been made to the flat board (a somewhat unnatural substrate type for this highly arboreal species), lack of significance across all substrates does not preclude the significant adjustments made to relative decreases in pole diameter.

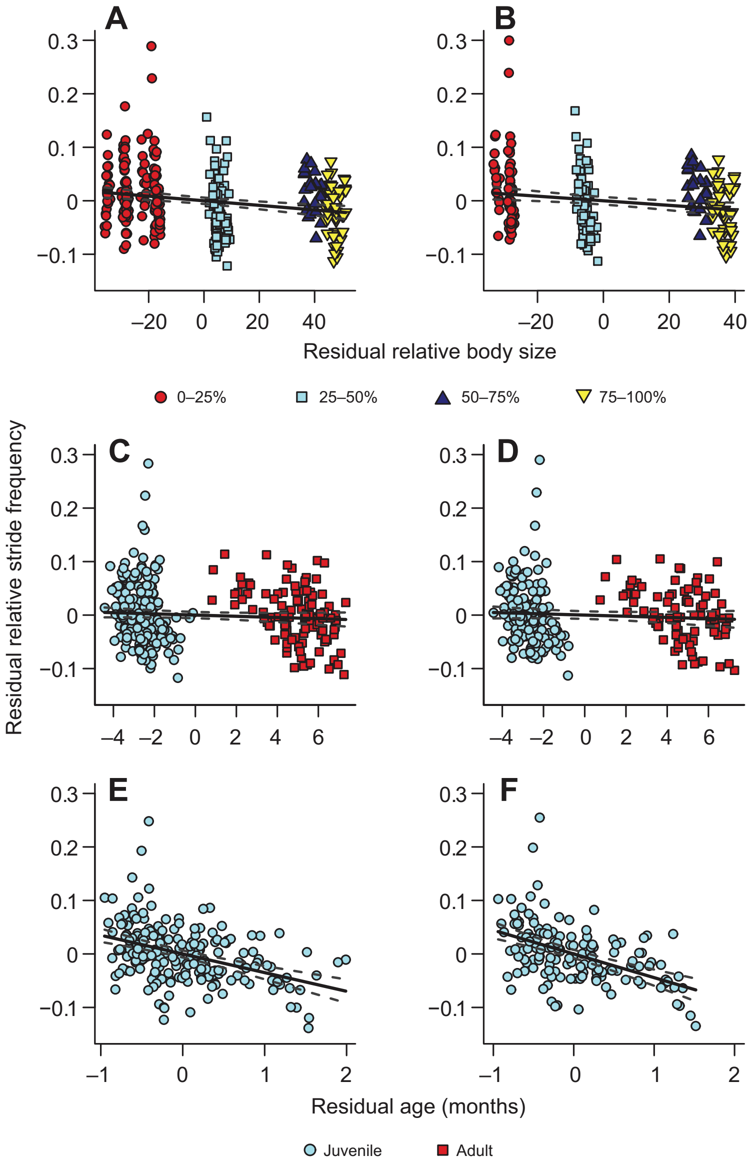

Fig. 6. Effects of relative body size and developmental age on relative stride frequency in *P. breviceps*. A–F illustrate the results of multiple regressions of relative stride frequency modeled as a function of relative body size, age in months and Froude number. The multiple regression analysis was performed on continuous data, but for visual reference, data points were grouped into four percentage categories representing relative body size (see Materials and methods) and two age categories. (A) Partial regression plot of relative stride frequency *vs* relative body size for locomotion across all substrates, controlling for age in months and Froude number. (B) Partial regression plot of relative stride frequency *vs* relative body size for locomotion on the poles alone, controlling for age in months and Froude number. (C) Partial regression plot of relative stride frequency *vs* age in months for locomotion across all substrates, controlling for relative body size and Froude number. (D) Partial regression plot of relative stride frequency *vs* age in months for locomotion on poles alone, controlling for relative body size and Froude number. (E) Partial regression plot of relative stride frequency *vs* age in months for locomotion across all substrates in juveniles alone, controlling for relative body size and Froude number. (F) Partial regression plot of relative stride frequency *vs* age in months for locomotion on poles in juveniles alone, controlling for relative body size and Froude number.

Functionally, by increasing limb contact time relative to stride duration, increased duty factor (at a given relative speed) should enhance stability on arboreal substrates by increasing the relative duration of grasping and by minimizing substrate displacement (Schmitt, 1999; Stevens, 2006). Indeed, in some primates, duty factor has been shown to increase on poles compared with floors, on smaller compared with larger poles, and on declines (Schmitt, 1999; Stevens, 2003; Young, 2009b). *Monodelphis domestica* and *Rattus norvegicus*, both terrestrially adapted mammals, also increase duty factor on a pole compared with a flat surface (Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). However, the relationship between duty factor and relative body to substrate size is not always consistent from a comparative perspective. For example, although strepsirrhine primates have been shown to use higher duty factors on smaller substrates, the effect of relative substrate size is subtle and variable across species (Stevens, 2003). Moreover, in opposition to predictions, Shapiro and colleagues (Shapiro et al., 2011) reported that in a natural habitat, squirrel monkeys (*Saimiri boliviensis*) used higher duty factors on broad arboreal supports compared with narrow ones. In the case of *Saimiri*, it was hypothesized that increased duty factor was a functional response to the difficulty of grasping large branch diameters in relation to hand or foot size. Thus, increases in duty factor at a given speed cannot strictly be interpreted as a response to a relatively small substrate diameter without consideration of the relationships among body size, substrate size and hand/foot size. Nevertheless, it seems reasonable to conclude that by increasing duty factor in response to relative decreases in pole diameter, sugar gliders were most likely enhancing their stability. Adjustments in limb phase occurred in response to the shift to a more graspable substrate, but not in response to relative decreases in substrate diameter *per se*. From a functional perspective, increasing limb phase within LSDC gait when switching from a flat board to a pole moves the limb sequencing closer to a pure ‘trot’. In a trot, contralateral limbs grasp the surface simultaneously (or near simultaneously), theoretically permitting the production of balanced torques to counter potential rolling moments (Prost, 1969; Preuschoft, 2002; Lammers and Gauntner, 2008; Young and Demes, 2010). Although limb phase itself was not influenced by the relative diameter of the poles, sugar gliders, regardless of age, used limb phase/duty factor combinations that enhanced their stability in the face of decreasing

Table 8. Multiple regression models testing the effects of log Froude number, relative body size and age on mean knee joint angle during stance phase in *P. breviceps*

| Regression model | *N* | Intercept | Regression coefficient | Standard error | *P*-value | Adjusted $R^2$ |
|---|---|---|---|---|---|---|
| All ages, all substrates | 112 | 51.658 | | | | 0.671 |
| log Froude number | | | –12.244 | 4.237 | 0.005 | |
| Relative size | | | 0.0559 | 0.0299 | 0.065 | |
| Age | | | 3.463 | 0.243 | <0.001 | |
| All ages, poles only | 81 | 54.677 | | | | 0.692 |
| log Froude number | | | –9.390 | 5.200 | 0.075 | |
| Relative size | | | 0.00644 | 0.0396 | 0.871 | |
| Age | | | 3.772 | 0.286 | <0.001 | |
| Juveniles, all substrates | 82 | 61.127 | | | | 0.0218 |
| log Froude number | | | –9.473 | 5.558 | 0.092 | |
| Relative size | | | 0.0397 | 0.0370 | 0.286 | |
| Age | | | –0.0657 | 1.464 | 0.964 | |
| Juveniles, poles only | 57 | 63.249 | | | | 0.000 |
| log Froude number | | | –7.051 | 7.237 | 0.334 | |
| Relative size | | | 0.00903 | 0.0522 | 0.863 | |
| Age | | | 0.348 | 1.950 | 0.859 | |

relative pole diameter by increasing the number of supporting limbs used throughout the stride.

Primates have relatively long strides and low stride frequencies at a given speed compared with cursorial and some non-cursorial mammals (Alexander and Jayes, 1983; Alexander and Maloiy, 1984). These stride characteristics have been considered to be part of a complex of features associated with 'compliant' gait, which benefits arboreal locomotion and enhances stability by reducing substrate reaction forces on limbs and minimizing branch oscillations (Demes et al., 1990; Schmitt, 1999). It has not been well established, however, how stride length or stride frequency of other arboreal mammals compares with that of primates or how substrate diameter influences these stride characteristics. However, if these features are advantageous on 'small branches', a reasonable prediction is that stride length should increase and stride frequency should decrease as substrate size decreases. Our data on sugar gliders is consistent with that prediction, supporting the association of these stride characteristics with navigation of relatively small substrates. Delciellos and Vieira compared relative stride lengths among seven species of terrestrial and arboreal didelphids moving across a flat surface *vs* cylindrical supports of four diameters (Delciellos and Vieira, 2006; Delciellos and Vieira, 2007). The arboreal taxa used relatively longer strides on the thinnest supports compared with terrestrial taxa, but differences in relative stride length within

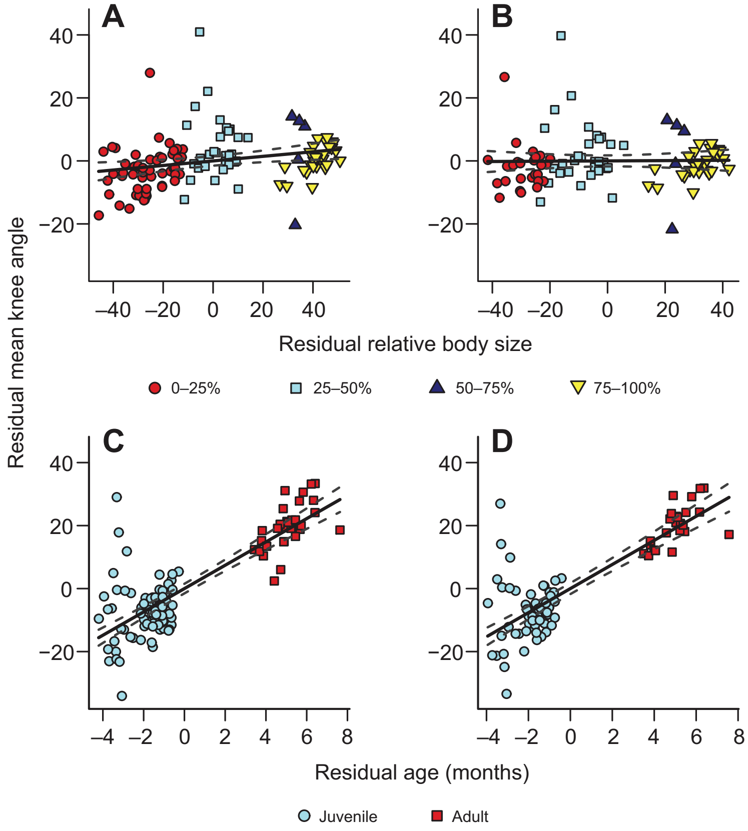

Fig. 7. Effects of developmental age and relative body size on mean knee joint angle during stance phase in *P. breviceps*. A–D illustrate the results of multiple regressions of mean knee joint angle modeled as a function of relative body size, age in months and Froude number. The multiple regression analysis was performed on continuous data, but for visual reference, data points were grouped into four percentage categories representing relative body size (see Materials and methods) and two age categories. (A) Partial regression plot of mean knee angle *vs* relative body size for locomotion across all substrates, controlling for age in months and Froude number. (B) Partial regression plot of mean knee angle *vs* relative body size for locomotion on the poles alone, controlling for age in months and Froude number. (C) Partial regression plot of mean knee angle *vs* age in months for locomotion across all substrates, controlling for relative body size and Froude number. (D) Partial regression plot of mean knee angle *vs* age in months for locomotion on poles alone, controlling for relative body size and Froude number.

arboreal or terrestrial taxa did not exhibit a clear pattern with respect to substrate diameter. In contrast, the arboreal lizard *Anolis sagrei* increases its stride length as substrate diameter increases (Spezzano and Jayne, 2004). Postural differences among vertebrates make direct comparison between reptiles and mammals problematic. Nevertheless, more comparative research would facilitate our understanding of the functional implications of stride length in an arboreal context.

Limb flexion, especially at or near mid-stance, lowers the body's center of mass and is thus beneficial to an animal balancing on an arboreal substrate (Cartmill, 1985; Schmitt, 1999; Preuschoft, 2002; Schmitt, 2003a; Schmidt, 2005; Schmidt and Fischer, 2010). Accordingly, arboreal taxa such as primates (Schmitt, 2003a; Schmidt, 2005) and some arboreal lizards [*C. calyptratus* (Higham and Jayne, 2004), *Anolis sagrei* (Spezzano and Jayne, 2004)] have been shown to increase limb flexion in response to decreasing substrate diameter. This kinematic response has also been reported in non-arboreal rats (*R. norvegicus*) when tested on poles of decreasing diameter (Schmidt and Fischer, 2010). In contrast to these other taxa, and contrary to our prediction, sugar gliders did not adjust their knee flexion in response to relative decreases in pole diameter, while adults, but not juveniles, counter-intuitively exhibited a tendency toward more flexed knees on the flat board rather than on the poles. Although the sugar gliders did not for the most part adjust their knee flexion in the face of relative decreases in substrate size, this does not preclude the fact that their limbs were flexed at the knee on all substrates sampled, especially with respect to the more pronounced knee flexion in the juveniles (Table 2). It is possible that this species' ability to grasp with hands and feet, in conjunction with flexion at the knee, was sufficient for stability, even on the relatively smallest substrates. Moreover, adults might have used increased flexion on the flat board because they are unable to grasp it. Juveniles, with limbs already more flexed than those of adults (see below), perhaps had reached their limit of flexion. These hypotheses require further study, as the sample size for the knee joint angle values in adults was very reduced ($N$=31).

## Age affects quadrupedal kinematics in *P. breviceps*

### Juveniles *vs* adults

In conjunction with our analysis of the influence of relative body to substrate size on quadrupedal kinematics in sugar gliders, we also examined the influence of age on the same variables by holding relative body size and relative speed constant. As predicted, the quadrupedal walking of juvenile sugar gliders was not dynamically similar to that of adults. The age-related differences were not related to differences in body size *per se*; kinematic differences between juveniles and adults (or among juveniles; see below) were found even when differences in body size relative to substrate size (and relative speed) were controlled for.

Juveniles differed from adults with respect to several kinematic variables that were predicted to enhance stability on arboreal substrates. For example, at a given relative speed and relative body size, juveniles used lower limb phases than adults, and this, combined with their use of higher duty factors, resulted in juveniles being supported by more limbs on average during a stride compared with adults. Thus, limb phase values employed by juvenile sugar gliders can be interpreted as part of a functional complex with duty factor that serves to enhance walking stability. Even considered separately, the use of increased duty factor in juveniles compared with adults regardless of relative body size or speed promotes stability by increasing relative contact time with the substrate.

An ontogenetic transition in limb phase preference has also been demonstrated for other mammals such as rodents (Eilam, 1997), cats (Peters, 1983) and primates (Hildebrand, 1967; Rollinson and Martin, 1981; Hurov, 1982; Vilensky and Gankiewicz, 1989; Nakano, 1996; Dunbar and Badam, 1998; Shapiro and Raichlen, 2005; Shapiro and Raichlen, 2006). These transitions are in part associated with neurological maturation (Muir, 2000), but there is also evidence that limb phases preferred by juveniles compensate for growth-related changes in limb proportions or the position of the body's center of mass (Hildebrand, 1967; Rollinson and Martin, 1981; Peters, 1983; Blumberg-Feldman and Eilam, 1995; Shapiro and Raichlen, 2006). For example, at growth stages associated with increases in relative hindlimb length, kittens as well as infant baboons have been shown to shift to a LSLC walking gait (i.e. limb phases between 0% and 25%) (Peters, 1983; Shapiro and Raichlen, 2006) as a means to avoid ipsilateral forelimb–hindlimb interference (Hildebrand, 1968; Hildebrand, 1980). Our sample of juvenile sugar gliders exhibited strong positive allometry of hindlimb length (see below), but limb phase was not significantly influenced by age within juveniles. Therefore, it is unlikely that ontogenetic transitions in limb proportions account for the juveniles' preference for limb phase extending into the LSLC range. However, as discussed above, the limb phases used by juveniles increased their mean number of limbs in support during a stride, and were thus likely used as a means to increase stability (Vilensky and Gankiewicz, 1989).

Juveniles used more flexion at the knee on average during stance phase than adults, regardless of relative body size or substrate type (board *vs* poles). In addition to using more flexion at the knee throughout stance phase, juveniles also used more knee flexion at hindlimb lift-off than adults, as has been reported for other small mammals (Schilling, 2005). Because adjustments in hindlimb flexion were not specifically associated with movement on poles, or with relatively decreasing substrate diameter, more pronounced hindlimb flexion in juveniles is more likely to be due to immature limb muscle development than to enhancement of stability. However, this hypothesis would need to be confirmed by an ontogenetic analysis of limb muscle size and physiology in sugar gliders.

Our prediction that juveniles would use relatively longer strides and lower stride frequencies than adults was not met. Rather, for the most part, juveniles and adults showed no significant differences in relative stride length or relative stride frequency. Even the one significant difference observed (adults used significantly greater relative stride lengths than juveniles across all substrates) was opposite in direction to that predicted. It is possible that juveniles used relatively short strides compared with adults as a means to reduce vertical fluctuations of the body's center of mass (Muir et al., 1996; Muir, 2000; Delciellos and Vieira, 2007), but the lack of significant differences in relative stride length between juveniles and adults on poles alone, or in relative stride frequency across any substrate, weakens this hypothesis.

### Age-related changes within juveniles

For all variables except limb phase and hindlimb flexion at the knee, the ontogenetic differences observed across the juvenile–adult sample extended to comparisons among juveniles of different ages. In contrast, hindlimb flexion did not vary significantly among juveniles, suggesting that the juvenile ages we sampled post-dated ages at which hindlimb flexion might have been more pronounced, or preceded the transition to more adult-like hindlimb flexion angles. Although age did not affect limb phase within juveniles, younger juveniles used significantly higher duty factors than older juveniles, and were supported by more limbs on average during a stride. The trends within juveniles for duty factor and limb support were thus similar to the trends found when juveniles were compared with adults, and suggest an inverse relationship between age and the need for stability brought about by long limb contact times and a greater number of supporting limbs (Vilensky and Gankiewicz, 1989; Cartmill et al., 2002).

However, whereas the combined juvenile–adult sample showed little to no difference in relative stride length or stride frequency, the juvenile sample showed highly significant increases in relative stride length and decreases in relative stride frequency as age increased. This result contrasts with our prediction that younger juveniles would use relatively longer strides and lower stride frequencies as a stabilizing mechanism (i.e. to reduce substrate displacement, which would be exacerbated by short strides with high stride frequencies). Although juveniles did not differ significantly with respect to hindlimb flexion, their hindlimbs grew with positive allometry (reduced major axis regression of log thigh+leg length on log body mass: slope=0.49, $P<0.001$, $R^2=0.70$, 95% confidence intervals=0.39–0.60). Therefore, the relatively short limbs of the youngest juveniles most likely account for these age-related trends, as relatively short limbs would reduce relative stride length, leading to higher relative stride frequencies at a given relative speed. In other words, it is possible that differences between younger and older juveniles in these stride characteristics are a by-product of differences in relative limb length, rather than a functional compensation.

As discussed above, increasing stride length while decreasing stride frequency is a functional response to relative decreases in substrate diameter. Thus, if relatively long strides and low stride frequencies are an adaptive advantage for moving along relatively narrow (and potentially unstable) arboreal substrates, we conclude that the youngest juvenile sugar gliders (using relatively shorter strides and higher stride frequencies) would be at a potential disadvantage when navigating substrates on which they are the same relative size as older juveniles.

In contrast to our results, Raichlen found the opposite trend within a sample of infant primates (baboons); older infants used relatively shorter strides and higher stride frequencies than younger infants (Raichlen, 2005a). Raichlen attributed the long strides and low stride frequencies of the youngest infants to a biomechanical by-product of distally distributed limb muscle mass brought about by the importance of grasping to the mother early in infancy. The difference between our results and those reported for primates may reflect the (more advanced) ages represented by our juvenile sample, the infrequent clinging to parents at this stage, and/or the less developed grasping musculature in sugar gliders compared with primates. Further research addressing limb inertial properties in sugar gliders would be needed to resolve these issues.

## CONCLUSIONS

This study contributes new data to a growing body of comparative literature addressing kinematic responses of (adult) small-bodied mammals to arboreal substrates, including those that are arboreally adapted with grasping extremities (Pridmore, 1994; Schmitt, 2003b; Schmitt and Lemelin, 2004; Delciellos and Vieira, 2006; Stevens, 2006; Delciellos and Vieira, 2007; Scheibe et al., 2007; Stevens, 2007; Nyakatura et al., 2008; Nyakatura and Heymann, 2010) and those that lack grasping capability and are predominantly terrestrial (Lemelin et al., 2003; Lammers and Biknevicius, 2004; Lammers, 2007; Lammers and Gauntner, 2008; Lammers, 2009; Schmidt and Fischer, 2010; Lammers and Zurcher, 2011). Much insight on arboreal adaptations has been gained from these studies, but this study is one of very few to provide ontogenetic kinematic data for mammals in an arboreal context (e.g. Young, 2009a; Young, 2009b).

Overall, our findings support our predictions. In most cases, sugar gliders adjusted locomotor kinematics in ways that provided enhanced stability, either for movement on relatively small substrates or as a compensation for presumed immature neurological and musculoskeletal development in juveniles. Our results have implications for interpreting the locomotion of juveniles in a natural habitat. That is, if a smaller juvenile were on the (absolutely) same size branch as an adult, the juvenile would be relatively smaller, and thus its kinematics would differ as a result of the effects of both relative size and age. If the juvenile were moving on a substrate on which it was the same relative size as an adult, its kinematics would differ, but only as a consequence of the influence of age. Finally, a juvenile moving from a relatively large substrate to a smaller substrate would adjust its kinematics in ways similar to that of an adult. Field research on substrate preference in sugar gliders during ontogeny is needed to fully evaluate selective pressures that may be unique to juveniles of this species. Nevertheless, this study has shown that although substrate variation in an arboreal environment presents similar challenges to all individuals, regardless of age or absolute body size, neuromuscular immaturity confers unique problems to growing animals, requiring kinematic compensation.

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