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REVIEW

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Going the distance: The biomechanics of gap-crossing behaviors

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Abstract

The discontinuity of the canopy habitat is one of the principle differences between the terrestrial and arboreal environments. An animal's ability to cross gaps—to move from one support to another across an empty space—is influenced by both the physical structure of the gap and the animal's locomotor capabilities. In this review, we discuss the range of behaviors animals use to cross gaps. Focusing on the biomechanics of these behaviors, we suggest broad categorizations that facilitate comparisons between taxa. We also discuss the importance of gap distance in determining crossing behavior, and suggest several mechanical characteristics that may influence behavior choice, including the degree to which a behavior is dynamic, and whether or not the behavior is airborne. Overall, gap crossing is an important aspect of arboreal locomotion that deserves further in-depth attention, particularly given the ubiquity of gaps in the arboreal habitat.

KEYWORDS
arboreal locomotion, biomechanics, gap crossing

1 | INTRODUCTION

The discontinuity of the canopy habitat is one of the principle differences between the terrestrial and arboreal environments (Cartmill, 1974). An animal's ability to cross gaps—to move from one support to another across an empty space—is influenced by both the physical structure of the gap and the animal's locomotor capabilities (Cannon & Leighton, 1994). As canopy connectivity is a significant predictor of arboreal pathway use and habitat selection (Hopkins, 2011; Madden, Garber, Madden, & Snyder, 2010), increased performance at gap crossing could enable animals to use more direct paths through the forest, reducing total path length and leading to selective advantages (Cant, 1992; Temerin & Cant, 1983). However, much of what we know about arboreal locomotion concerns movement *on* branches (e.g., Karantanis, Rychlik, Herrel, & Youlatos, 2017), rather than movement *between* branches (e.g., Jayne & Riley, 2007). Given the ubiquity of gaps in the arboreal habitat, it is worth considering how the biomechanics of on-branch locomotion translates to the biomechanics of gap crossing.

In general, arboreal animals exhibit a high degree of locomotor diversity, potentially driven by the complexity of the arboreal habitat (Granatosky, 2018). Animals make choices between the different movement behaviors in their repertoires, and these choices can often be related to energy- or time-savings. Malaysian colugos, for example, appear to save time by gliding rather than climbing through the canopy (Byrnes, Libby, Lim, & Spence, 2011), and ground squirrels may save both time and energy by running instead of walking when moving around their home range (Kenagy & Hoyt, 1989). When crossing gaps, animals must furthermore choose behaviors that enable them to cover sufficient distances, or risk falling short of their target. But although many studies have considered how arboreal animals might avoid falling off of branches during arboreal locomotion (e.g., Byrnes & Jayne, 2014; Higurashi, Hirasaki, & Kumakura, 2009; Jusufi, Goldman, Revzen, & Full, 2008; Schmidt & Fischer, 2010), how these strategies might relate to gap crossing, or vary with varying gap distance, has rarely been examined.

Nevertheless, the limited data from a range of taxa suggest potential trends that link gap distance with behavior. In this review, we describe these trends, and discuss the biomechanical principles that may help to explain them. We begin by discussing what types of obstacles are appropriately called "gaps," and suggest a broad categorization for the range of gap-crossing behaviors so far described in the literature. Then, we describe several characteristics of gap-crossing behaviors that appear to vary with gap distance. Finally, we consider how mechanical considerations may help explain patterns of behavior use with gap size, including morphological and structural factors.

2 | WHAT IS A GAP?

The term "gap" is rarely defined in the animal locomotion literature, but commonly refers to treefall or canopy gaps in the field of forest ecology: holes in the uppermost canopy layer that often extend to the ground, allowing light to penetrate into lower forest layers (Brokaw, 1982; Hubbell & Foster, 1986). An alternative ecological definition was suggested by Connell, Lowman, and Noble (1997): A gap is any "space temporarily left unoccupied in an assemblage of sessile organisms." In this review, our focus is on the biomechanical consequences of gaps on animal locomotion, and as such, it is the physical space itself that matters most, regardless of what type of support defines the gap. We therefore consider a gap to be any empty space occurring at a range of scales (Connell et al., 1997; Dial, Nadkari, & Cushing, 2004; Lieberman, Lieberman, & Peralta, 1989), including large clearings between forest patches and small-scale discontinuities between branches and trees (Figure 1). In particular, we focus on gap crossing that involves movement from one support to another, typically across spaces that are roughly similar to the body size of the animal.

Although the existing literature on gap crossing has tended to focus primarily on relatively large, horizontal gaps (Blaesing & Cruse, 2004; Gart, Yan, Othayoth, Ren, & Li, 2018; Jayne & Riley, 2007; Pick & Strauss, 2005), some studies on snakes and rodents have considered vertical gap-crossing movements as well (Hoefer & Jayne, 2013; Jorgensen & Jayne, 2017; Youlatos, 1999), so we consider gap crossing to include movement in a variety of directions. In general, gap crossing shares characteristics with a range of behaviors that involve transitioning from one surface or support to another, such as stepping up or down on uneven terrain, as these behaviors also

FIGURE 1 Forest gaps of different scales. (a) Large-scale gaps from human construction can separate patches of continuous forest. (b) A tree fall can create gaps in the canopy. (c) The structure of plants can create fine-scale gaps for animals to navigate (as seen in this northern muriqui, *Brachyteles hypoxanthus*). Photo credits: (a) T. R. Shankar Raman [CC BY-SA 4.0], from Wikimedia Commons, (b) Tim McCormack [CC BY-SA 4.0], from Wikimedia Commons, (c) Kenny Ross (Flickr) [CC BY-SA 2.0], via Wikimedia Commons [Color figure can be viewed at wileyonlinelibrary.com]

involve movements from one support to another across an empty space.

Not all physical gaps present locomotor challenges to all animals: a 5 mm gap is not crossable by a fruit fly (Pick & Strauss, 2005), but might be unnoticeable to a primate. We suggest that a gap becomes ecologically relevant when crossing it requires a change in the animal's locomotor kinematics (i.e., there is a change in locomotion pattern between pre-gap and during-gap movement), or if negotiating the gap requires anticipatory behaviors. To determine when a gap is ecologically relevant requires experimental investigation. One approach might be to conceal gaps of various size from an animal as it crosses over the gap, and identify when deviations from normal gait patterns occur (e.g., Daley, Usherwood, Felix, & Biewener, 2006).

3 | CATEGORIES OF GAP-CROSSING BEHAVIORS

Of the species studied so far, most exhibit more than one type of gap-crossing behavior. Although there is great variation across species, we suggest the following groupings to facilitate broader comparisons: stepping/reaching, jumping/lunging, swinging, flying/gliding, and assisted behaviors. Some example behaviors are shown in Table 1.

3.1 | Stepping/reaching

3.1.1 | Limbed reaching

Limbed reaching behaviors are those in which an animal uses a limb to make initial contact with the target substrate, and then transfers itself onto that substrate. Familiar limbed reaches include the reaching behaviors of quadrupeds such as primates, frogs, or squirrels, in which the animal makes initial contact with the target using a single forelimb (e.g., Youlatos & Samaras, 2011). This category also includes other limb-driven maneuvers, such as bimanual pullups in primates (K. D. Hunt et al., 1996). Some species can reach from a below-branch, suspended posture, including sloths (Granatosky, Karantanis, Rychlik, & Youlatos, 2018) and some primates (e.g., Cant, Youlatos, & Rose, 2003).

3.1.2 | Stepping or walking

Various walking-like behaviors can be used to transfer between branches. Clambering, or irregular/cautious climbing, generally involves movement between supports (K. D. Hunt et al., 1996; Youlatos & Samaras, 2011). Many other non-airborne arboreal movement gaits, including quadrupedal and bipedal walking and running, scrambling, and various suspensory movements, can be recruited for both between- and on-branch locomotion (K. D. Hunt et al., 1996).

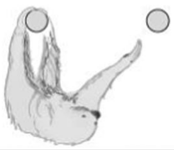
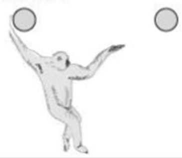
3.1.3 | Whole-body reaching

Whole-body reaches involve extending the head outward over the gap and toward the target. Cantilever bridges in snakes are the best-studied whole-body reaching behavior (Byrnes & Jayne, 2012; Jayne & Riley, 2007; Jayne, Lehmkuhl, & Riley, 2014; Jorgensen & Jayne, 2017; Mansfield & Jayne, 2011; Mauro & Jayne, 2016). Some birds also use this behavior to cross short gaps by leaning out over the gap, grasping the target support with their beak, and pulling themselves across the gap, using the beak as a sort of "third foot" (Zeffer, 2003). Finally, bridging behaviors, even in limbed animals, can be more similar to whole-body reaches than to limb reaches; cockroaches, for example, appear to rely on head contact more than limb contact when crossing gaps (Gart et al., 2018).

3.2 | Jumping/lunging

Jumping involves pushing off from a substrate and becoming airborne (Gordon, Blickhan, Videler, Dabiri, & John, 2017). Primates, for

TABLE 1 Examples of different gap-crossing behaviors

Category	Reaching/Stepping	Reaching/Stepping	Jumping/Lunging	Jumping/lunging	Swinging	Flying/Gliding
Example behavior	Single limb reach 	Cantilever bridge 	Quadrupedal lunging 	Jumping 	Brachiation 	Flying 
Quasistatic or dynamic?	Quasistatic	Quasistatic	Dynamic	Dynamic	Dynamic	Dynamic
Airborne phase?	No	No	No	Yes	Sometimes	Yes
Controlled contact speed?	Yes	Yes	No	Sometimes	No	Yes
Used by...	Various limbed animals	Snakes	Various limbed animals	Various limbed animals	Some primate species	Birds, bats, insects

example, use a variety of leaping behaviors to cross gaps (K. D. Hunt et al., 1996). Lunges also involve propulsive movements, but do not become airborne (as in an "incomplete leap," Fontaine, 1990; K. D. Hunt et al., 1996). Jumps can take a variety of forms (see Gordon et al., 2017 for a detailed mechanical analysis), including many-legged jumps by spiders (Hill, 2006) and legless lunging and jumping in some snakes (Graham, Weiss, Jayne, & Socha, 2016; Jayne & Riley, 2007).

3.3 | Swinging

Swinging involves a pendulum-like mechanism in which the animal rotates around a pivot point. The brachiating locomotion of some primate species, in which the animal's body pivots about a handhold, is a well-known example of a swinging behavior. Primates can also use other, non-brachiating, swinging behaviors to cross gaps, such as tail swinging and forelimb swinging (K. D. Hunt et al., 1996). Swinging has also been observed in one bird species, the Puerto Rican spindalis, which can use its beak as the pivot to swing between closely spaced lianas (Williams & Bunkley-Williams, 2006).

3.4 | Flying/gliding

Flying and gliding are not typically considered in the context of gap crossing, as these airborne behaviors are generally conceptualized as behaviors used for longer distance travel (Dudley et al., 2007; Socha, Jafari, Munk, & Byrnes, 2015). However, many arboreal animals frequently cross intermediate distances between perches using aerodynamic behaviors, including short flights, bimodal hopping/flying (Heers & Dial, 2015), or flight-assisted hopping (Chin & Lentink, 2017). Additionally, gliding between supports is a gap-crossing behavior in arboreal species, but because many gliders require an initial falling phase before appreciable lift is produced (Socha et al., 2015), gliding is only effective for gaps of particular sizes or orientations. Taxonomically, gliding is used by a large range of groups, including mammals, reptiles, arthropods, and amphibians (Socha et al., 2015), whereas flapping flight is restricted to bats, birds, and insects (Alexander, 2003). Generally, there have been few studies of gap-crossing in flapping flyers at scales on the order of a few body lengths (but see Chin & Lentink, 2017), and studies of gliding across smaller gaps have focused on squirrels (Ando & Shiraishi, 1993; Paskins, Bowyer, Megill, & Scheibe, 2007; Stafford, Thorington, & Kawamichi, 2002).

3.5 | Assisted behaviors

A final category of gap-crossing behavior involves movements in which the animal interacts with another individual or material for assistance. Spiders, for example, may create bridges of web to cross from one support to another across a gap (Wolff et al., 2014), and are thus assisted by the thread. Animals may also recruit companions to help them cross gaps. For example, infant primates may hitch a ride on their parent for gap crossing (K. D. Hunt et al., 1996), and army ants can make bridges formed of large groups of ants holding on to each other (Anderson, Theraulaz, & Deneubourg, 2002). Finally, primates may use branch and tree compliance to assist in their gap-crossing behaviors, as in pumping leaps (K. D. Hunt et al., 1996) or the tree-swaying behaviors of orangutans. This latter behavior can be used to move between trees, and the whole body of the orangutan acts to swing the supporting tree or limb, thereby bending it closer to the target (Cant, 1987; Halsey, Coward, & Thorpe, 2016; Thorpe, Crompton, & Alexander, 2007).

4 | PATTERNS OF BEHAVIOR USE WITH INCREASING GAP SIZE

Existing examinations of gap crossing, including multiple studies of snakes (e.g., Jayne & Riley, 2007), primates (e.g., Cannon & Leighton, 1994), and birds (e.g., Chin & Lentink, 2017; Robinson & Holmes, 1984), demonstrate that many animals change behavior to cross gaps of increasing size. The information summarized in Table 2 suggests a few key factors that may help illuminate distance-related changes in behavior. Although there is little data available on how behavior transitions with gap distance, we propose that these transitions relate to whether or not a behavior involves high accelerations, has an airborne phase, or enables the animal to control the speed at which it contacts the target.

4.1 | Dynamic behaviors are used to cross larger gaps

Some gap-crossing behaviors involve minimal accelerations, such as slow bridging in snakes (Jayne & Riley, 2007). Such behaviors can be treated quasi-statically during mechanical analysis; that is, forces and moments at each instant of the behavior can be approximated to be in static equilibrium. In contrast, jumping, swinging, and flying are more dynamic and involve appreciable accelerations and control of momentum. Several species listed in Table 2 appear to use quasistatic behaviors for relatively small gaps, and recruit more dynamic behaviors for larger gaps (Arkley, Tiktak, Breakell, Prescott, & Grant, 2017; Cannon & Leighton, 1994; Jayne & Riley, 2007), a pattern that may be general. Yet, few studies have systematically presented animals with gaps of increasing size, which is necessary for investigating whether and how transitions occur. Such studies, particularly when paired with kinematic analysis, electromyography, or supports instrumented to record forces, would shed light on this question.

4.2 | Non-airborne behaviors are limited to shorter gap distances than airborne behaviors

A behavior has an airborne phase if there is a portion of time in which the animal has left the origin substrate but not yet contacted the target substrate. Jumping, gliding, and flying are definitionally airborne, but other behaviors may have airborne phases as well. High-speed brachiation, for example, can become "ricochetal,"

TABLE 2 Existing data relating behavior and distance. Distance regimes for multiple behaviors in a single species are only known in a few cases (top). The table summarizes the distances at which various behaviors have been recorded, either set distances recorded in the lab or a median or average from the field. Some additional data (bottom) show a range of behavioral modifications with increasing distance

Multiple behaviors and specific distances

Species	Behavior 1	Distance crossed	B2	D2	B3	D3	B4	D4	Citation
Bornean agile gibbon (*Hylobates agilis*)	Leaping	3.0 m^{b}	Brachiation (all types)	2.5 m^{b}	Bridging	1.5 m^{b}	Bipedal walking	1.0 m^{b}	(Cannon and Leighton, 1994), (Bertram and Chang, 2001)
			Constant-contact brachiation	0.8, 1.2 m^{d}					
			Ricochetal brachiation	1.6, 1.72, 1.95, and 2.25 m^{d}					
Long-tailed macaque (*Macaca fascicularis*)	Leaping	1.5 m^{b}	Bridging/scrambling/ climbing/hopping	0.5 m^{b}	Quadru-pedalism	0.1 m^{b}			(Cannon and Leighton, 1994)
Japanese giant flying squirrel (*Petaurista leucogenys*)	Gliding	>3.0 m^{c} (~30 m)^{a}	Assisted jumping	~1-3 m^{c}	Jumping	<1.0 m^{c}			(Ando and Shiraishi, 1993)
Pacific parrotlet (*Forpus coelestis*)	Flap-bounding flight	70 cm^{d}	Continuous flapping, flight- assisted jump	40 cm^{d}	Jumping	20 cm^{d}			(Chin and Lentink, 2017)
Fruit flies (*Drosophila melanogaster*)	Climbing	2.0 - 4.3 mm^{c}	Normal walking	Up to 2.0 mm^{c}					(Pick and Strauss, 2005)

Single behaviors or general distances

Species	Behavior(s)	Distances	Influence of increasing gap distance, max performance if known.	Citation
Stick insects (*Aretaon asperrimus*)	Stepping	30, 50 mm^{d} (longest crossable distance for most males)	Leg position shifts rearwards, lower amplitude of initial leg swing. 50 mm is maximum crossable distance for the males (approx. = to body length).	(Blaesing and Cruse, 2004)
Cockroaches (*Blaberus discoidalis*)	Bridging (with head contact).	0.2 to 1 body lengths^{c} (BL ~ 5cm)	Increased risk of falls due to pitching. Below 0.6 BL, crosses always successful. Cockroaches cannot cross gaps > 1 BL.	(Gart et al., 2018)
Jumping spiders (*Phidippus princeps* and *Phidippus regius*)	Jumping	3, 6 cm^{d} (*P. princeps*) 3 - 7.5 cm^{c} (*P. regius*).	More dragline braking. Trajectory changes from flat to steep (energetically optimal). Some species of salticid spiders can jump up to 16 cm.	(Hill, 2006; Nabawy et al., 2018)
Brown tree snake (*Boiga irregularis*)	Bridging and lunging	Up to ~ 50-60% snout-vent length^{c}	Lunging occurs more frequently (particularly at limit of bridging ability). Largest gap size (relative): 64% SVL (43 cm SVL snake) Largest gap size (absolute): 81 cm (165 cm SVL snake)	(Jayne and Riley, 2007)
Dormouse (*Muscardinus avellanarius*)	Reaching and jumping	Up to 28 cm^{c}	Increased use of jumping over reaching, increased avoidance of gap.	(Arkley et al., 2017)
Colugos (*Galeopterus variegatus*)	Gliding	2.5 – 150 m^{c}	Decreased landing forces	(Byrnes et al., 2008)

(Continues)

TABLE 2 (Continued)

Species	Behavior(s)	Distances	Influence of increasing gap distance, max performance if known.	Citation
Single behaviors or general distances				
Didelphid marsupials (multiple species)	Jumping	40, 60, 80, 100 cm[d]	Bridging may occur at smaller distances in some species. Use of tail in one species at larger gap sizes (*Micoureus paraguayanus*).	(Delciellos and Vieira, 2009)
Two-toed sloth (*Choloepus didactylus*)	Bridging, suspensory clambering	Unspecified	Increased use of bridging over clambering.	(Granatosky et al., 2018)

[a] mean distance observed in field

[b] median distance observed in field

[c] range observed/tested in field or lab

[d] specific distances tested in lab/captivity

involving a stage in which the animal releases its initial handhold before grasping the next (Bertram, Ruina, Cannon, Chang, & Coleman, 1999). In theory, behaviors with an airborne phase should present a greater risk of falling and involve higher take-off and landing speeds than non-airborne behaviors, a target for future investigation.

Typically, airborne behaviors are used for crossing larger gaps, although some animals with specialized morphologies do not appear to use airborne behaviors at all, including the slow loris (Sellers, 1996) and most snakes (Hoefer & Jayne, 2013; Lillywhite, LaFrentz, Lin, & Tu, 2000; Ray, 2012). It is not clear whether any animal has exclusively airborne behaviors in its gap-crossing repertoire. One candidate might be the hummingbird, whose short legs and decreased musculature (Zusi, 2013) could make crossing gaps via reaching difficult, but whether these birds sometimes maintain contact with the origin support during gap crossing is unknown.

4.3 | The ability to control contact speed differs between behavior types

Animals do not always control their landings, as illustrated by the "belly flop" landings of basal frogs (Essner, Suffian, Bishop, & Reilly, 2010). Non-aerodynamic airborne behaviors such as jumping are often approximately ballistic (Biewener & Patek, 2018), and as such the speed at landing is strictly correlated with the distance travelled. To deviate from such a trajectory at landing requires braking or repositioning behaviors, such as the use of stalling behaviors in gliding squirrels (Paskins et al., 2007) or drag lines in spiders (Hill, 2006, 2010; Nabawy, Sivalingam, Garwood, Crowther, & Sellers, 2018).

Fast behaviors may also incur reduction of control at landing, even when the animal maintains contact with the origin support. For example, brown tree snakes can gain extra distance during gap crossing by lunging toward the target, which involves an acceleration phase, but no airborne period (Jayne & Riley, 2007). During lunges, the velocity of the head is nearly 10 times the speed attained in cantilever bridges, and increased speed is generally associated with greater variability in the position of the head at landing (Jayne et al., 2014). Given that arboreal targets can be small and unstable, landing control could be a key factor influencing behavior choice during gap crossing, favoring the use of slower or non-airborne behaviors when possible.

To evaluate such hypotheses, further investigation is needed in several areas. First, the gap-crossing repertoires of a wider range of taxa should be documented, including information about how behavior varies with gap size. Studies in controlled environments, in particular, would help isolate the influence of distance from other contextual factors. Secondly, airborne and non-airborne behaviors should be compared within species, to understand what motivates the use of one type of behavior over the other. Finally, studies of landing control during gap crossing could be performed, particularly in animals that can be trained to perform different behaviors at the same distance, or the same behavior at multiple speeds. Despite the limitations of the existing data, we suggest a working hypothesis:

behaviors in which contact speed can be controlled are used when possible, but if such behaviors are non-airborne, they are inherently distance limited. In the following section, we present biomechanical considerations that help support this view.

5 | BIOMECHANICAL FACTORS INFLUENCING GAP-CROSSING BEHAVIOR

5.1 | Distance limitations of non-airborne behaviors

Non-airborne behaviors are intrinsically limited to gap distances smaller than the length of the animal itself, and in some cases the distance limitations may be even more restrictive. For example, the maximum length a snake could bridge without becoming airborne would be the length of its entire body, from snout to tail tip. But snakes do not reach this theoretical maximum, with the best-performing species exhibiting cantilever failure around 50% snout-vent length, SVL (Hoefer & Jayne, 2013; Lillywhite et al., 2000; Ray, 2012). What factors prevent animals from cantilevering farther?

The explanation for this limit comes from considerations of torque. As discussed by Jayne and Riley (Jayne & Riley, 2007), an animal in a cantilevered body position must hold itself up against two types of failure: pitching and buckling (Figure 2). First, considering the animal as a rigid beam, a pitching torque acts on the extended portion of the body, counterbalanced by the weight of the supported body and any stabilizing force the animal exerts. Stabilization against pitching might take a variety of forms. For example, humans use muscles such as the hamstrings and trunk extensors to maintain balance during short arm reaches, counteracting the forward shift of the center of mass (Kaminski & Simpkins, 2001; Tyler & Karst, 2004). Second, buckling will occur when the animal is unable to support the mass of the extended body or appendage, with bending occurring at one or more joints. As gap size increases, animals must put more of their body into an unsupported position to reach the target, exacerbating these effects. Once an animal has made contact with the target branch, it must still maintain stiffness to avoid excessive sagging, but the risk of pitching or buckling into the gap is decreased. These effects have been nicely illustrated in brown tree snakes, where muscle activity acts to prevent buckling (ventral flexion) before the snake's head makes contact with the target, at which point anti-sagging activity (dorsiflexion) begins (Jorgensen & Jayne, 2017).

Pitching is a particular risk for whole-body reaches. When more than 50% of the animal's body mass is extended over the gap, passive counterbalancing without grip is not physically possible. Evidence of the influence of pitching on gap-crossing performance can be found in snakes (Jayne & Riley, 2007) and cockroaches (Gart et al., 2018). The brown tree snake uses more tail wrapping during lunging than during cantilever bridges, where typically the weight of the animal on the origin support provides a passive counterweight against pitching (Jayne & Riley, 2007). Similarly, cockroaches pitch forward during gap crossing, and arrest this motion by making head contact with the target (Gart et al., 2018). When gaps are larger than 0.6 body lengths, cockroaches experience greater difficulty making this contact, and fall into the gap more frequently (Gart et al., 2018).

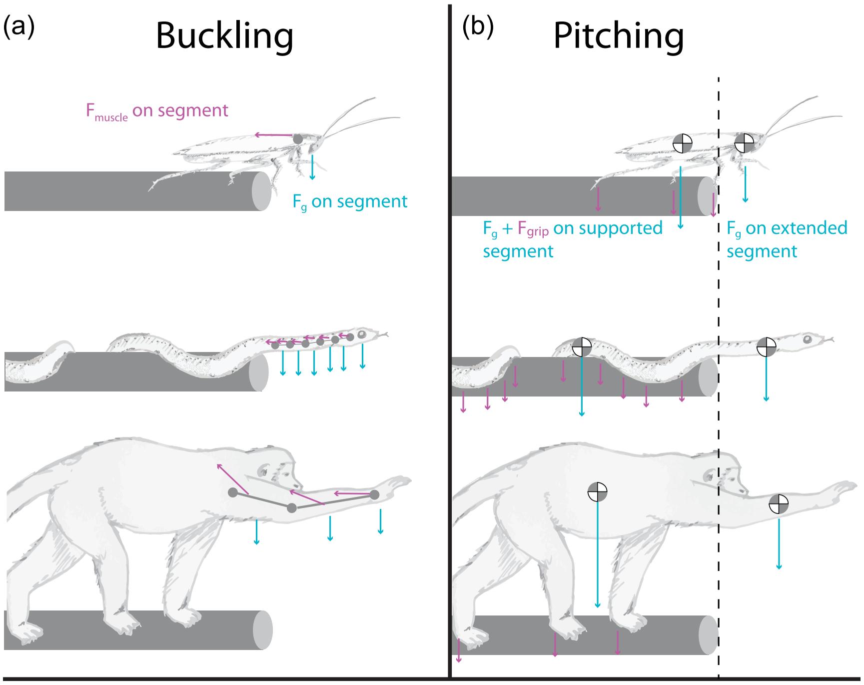


FIGURE 2 Torques associated with reaching behaviors. During above-substrate reaching, animals are subject to two primary challenges. First (a), they must maintain stiffness at each joint in the extended segment (typically a limb or the suspended portion of the body). Failure to maintain stiffness would cause buckling, and decrease the effective length of the extended portion of the body. Second (b), the animal must counter the rotational torque on the body due to the weight of the extended segment. This can occur passively if the supported portion of the animal weighs as much or more than the unsupported portion, but for sufficiently large gaps the animal must actively prevent itself from pitching forward [Color figure can be viewed at wileyonlinelibrary.com]

Animals reaching from a below-branch position also experience pitching torques, but in this case the torque acts to push the posterior of the animal toward, rather than off, the branch. Animals reaching from below the branch are also passively stable with respect to roll, exhibiting pendulum-like behavior (Hoefer & Jayne, 2013). In contrast, an animal that reaches from above the branch may create torques that tend to topple the animal, increasing the risk of falling. The torques associated with reaching from a suspended position have not been documented in any species, to our knowledge, so it is not clear how below-branch reaches compare to above-branch reaches, or how animals respond to torques while reaching from this position. It may be that animals cling more closely to the branch when reaching to take advantage of the normal force of the substrate to avoid rotations, or they may simply avoid extremely extended body positions altogether.

In the case of buckling, animals must hold their limbs or body in an sufficiently extended position to reach the target support, negotiating external forces as well as intersegmental mechanics (Hollerbach & Flash, 1982). In humans, reaching to more distant targets requires changes in the timing and intensity of associated muscular activity, with more distant targets requiring greater muscular effort to support more extended limb and body positions (Buneo, Soechting, & Flanders, 1994; Tyler & Karst, 2004). The forces involved will depend on the particular movements the animal uses to reach the target, and little data are available on how animals change limb kinematics to accomplish larger gap-crossing reaches. In contrast, reaching toward objects has received more attention, including one study on cats reaching for food, which demonstrated that cats primarily modulate elbow extension to increase reach height, although joint angles also decreased in the wrist and shoulder (Galloway & Koshland, 2002). The literature on the biomechanics of multisegmented reaching movements is rich with information that could be extended to consider gap-crossing movements, including examinations of muscular activity (e.g., Buneo et al., 1994; Tyler & Karst, 2004), kinematics (e.g., Martin, Cooper, & Ghez, 1995; Vandenberghe, Levin, De Schutter, Swinnen, & Jonkers, 2010), and control (in humans: Lackner & DiZio, 2009; and octopus: Sumbre, Gutfreund, Fiorito, Flash, & Hochner, 2001; Yekutieli, Sagiv-Zohar, Hochner, & Flash, 2005) and the influence of speed (e.g., Nishikawa, Murray, & Flanders, 1999), distance (e.g., Bonnefoy, Louis, & Gorce, 2009; Kaminski & Simpkins, 2001), and direction (e.g., Vandenberghe et al., 2010) on these variables. More studies exploring the application of these ideas to animals of varying morphology and reaching strategies is warranted.

These two torque challenges—avoiding pitching and avoiding buckling—provide a strength-based limit to the possible gaps an animal can span, in addition to the limit provided by the length of the animal's body or limbs. Different behaviors may be more subject to one type of constraint or the other. For example, because all snakes observed so far fail to maintain stiffness well before the theoretical length-maximum (Hoefer & Jayne, 2013; Jayne & Riley, 2007; Lillywhite et al., 2000), the maximum cantilevered length is likely limited by muscular strength. In contrast, a brachiating gibbon with arm length 0.56 m transitions from constant-contact brachiation (a non-airborne behavior) to ricochetal brachiation (an airborne behavior) at handhold spacings between 1.2 and 1.6 m (Bertram & Chang, 2001), very close to its geometrical maximum reach (twice arm length + torso width at shoulders). Constant-contact brachiation, then, may represent an example of distance limitation, where crossing ability is limited by the length of the limbs.

5.2 | Morphological specializations for reaching can only do so much

Morphological changes may help animals reach across larger distances. Simply increasing the length of the limbs, as in apes and monkeys (Preuschoft, Witte, Demes, & Matano, 1992), can help with length limitations to reaching ability. However, increasing limb length will also increase the moment of inertia, assuming geometric isometry (Preuschoft, 2002); a longer-armed animal would need to be able to produce larger torques to compensate for the additional mass. In the case of geometric isometry, torque scales as L^4, whereas muscle strength scales with cross-sectional area (L^2; Biewener & Patek, 2018). Thus as a limb increases in size, the muscles would eventually be too weak to support the larger limb. Consistent with this constraint, primates typically exhibit decreased relative limb length as body size increases (Jungers, 1985).

Distributing weight closer to the relevant point of rotation (Preuschoft, 2002) or changing the location of muscle attachment on the limb (Biewener & Patek, 2018) can help compensate for the increased torque associated with longer limbs. Lemurids and galagids, for example, exhibit positive allometry in the humerus and negative allometry in the radius, which likely moves the weight of the limb closer to the shoulder joint (Jungers, 1985). However, such alterations can have other disadvantages. For example, increasing the moment arm of a muscle increases its mechanical advantage, but also decreases the range of motion it can produce (Biewener & Patek, 2018).

Other strategies can help an animal avoid torque limitations associated with reaching. A lighter-weight limb would experience decreased torques, and some non-jumping animals such as the slow loris show significantly decreased thigh musculature compared to similarly sized jumping primates (Sellers, 1996). Vertebral morphology may also influence the ability of an animal to resist buckling torques; a stiffer spine would likely require less muscular effort to keep straight. In keeping with this idea, some primates that primarily bridge or cantilever exhibit relatively short intervertebral and intercostal spaces, which may be associated with trunk stability (Granatosky, Lemelin, Chester, Pampush, & Schmitt, 2014). More rigid spines may also benefit primates that employ suspensory locomotion (Granatosky, Tripp, Fabre, & Schmitt, 2016).

Morphological specializations for one gap-crossing behavior, though, can lead to trade-offs in other behaviors. For example, decreased spinal flexibility may be a disadvantage for leaping in primates (Shapiro & Simons, 2002). Given the competing constraints associated with different arboreal movements and the mechanical challenges associated with reaching, it is perhaps unsurprising that few animals appear to only use reaching to cross gaps.

5.3 | Distance, speed, and risk

The previous section discussed the challenges associated with the use of less dynamic, non-airborne reaching behaviors as gap size increases. A separate pattern is the tendency for animals *not* to use dynamic behaviors for the smallest gap sizes; eight of the species listed in Table 2 have a quasistatic behavior in their repertoire, and appear to use this behavior for smaller gap sizes. What considerations lead an animal to cease using a given behavior, both for gaps below and above a certain distance range?

For some dynamic behaviors, moving greater distances is associated with increased speed. In brachiating gibbons, for example, increasing handhold spacings leads to faster speeds and decreased contact times (Bertram & Chang, 2001). Under ballistic conditions, increased velocity at take-off leads to increased travel distance and landing velocity. Even in non-ballistic cases, increased distance may be associated with increased velocity. Grasshoppers, for example, exhibit greater jump distance when they increase take-off speed and modulate their in-air behavior (Hawlena, Kress, Dufresne, & Schmitz, 2011). In contrast, animals that can employ a braking mechanism of some kind may avoid increased landing speeds, such as when birds using aerodynamic forces to slow their speed at landing (Chin & Lentink, 2017), or when spiders use draglines to brake (Hill, 2006; Nabawy et al., 2018).

There are several costs associated with using behaviors where landing speeds are difficult to modulate, which may contribute to the decreased usage of these behaviors at shorter distances. First, animals could experience increased risk of falling, resulting from trade-offs between speed and accuracy. This risk should be increased for airborne behaviors, because losing contact with the origin substrate decreases the ability to recover if the animal misses the target (Cartmill, 1974), although we are not aware of any studies that explicitly compare falling frequency between different gap-crossing behaviors. Second, increased landing speeds and travel distances may also lead to increased landing forces, as in some frogs (Nauwelaerts & Aerts, 2006) and gliding squirrels (Paskins et al., 2007).

The potential for high landing forces during arboreal locomotion has led to one hypothesis regarding the evolution of gliding, that gliding behaviors may improve landing control during jumps (Paskins et al., 2007). The use of aerodynamic behaviors allows animals to have some degree of control of their landing speed and position, potentially avoiding costs associated with increased landing forces. Colugos, for example, use greater take-off forces when gliding greater distances, but the landing forces they experience are negatively correlated with glide distance (Byrnes, Lim, & Spence, 2008). However, because many gliding animals require some distance to build up speed before they begin generating appreciable lift, aerodynamic behaviors may be reserved for longer gaps, as in the Japanese giant flying squirrel, which primarily jumps for shorter gaps (<1 m; Ando & Shiraishi, 1993).

Animals capable of powered flight are less constrained by distance, as they can begin to generate aerodynamic forces nearly instantaneously (<0.2 s for Pacific parrotlets; Chin & Lentink, 2017). Nevertheless, flying animals often fly less and hop more in dense substrate or across short distances (Robinson & Holmes, 1982, 1984), thus the small distance limit appears to apply to these behaviors as well. Similarly, Pacific parrotlets will use different flying behaviors for different distances, including a hopping behavior for distances of ~30 cm, flapping flight for distances of ~40 cm, and flap-bounding flight for distances of ~70 cm (Chin & Lentink, 2017). In this case, the reason for hopping rather than flying over short distances may be related to energy use; a larger proportion of short flights are energetically intensive take-offs and landings. Generally, short flights may entail energetic costs more than twice that predicted by steady-state models of longer flights (Nudds & Bryant, 2000).

6 | PHYSICAL FEATURES OF SUPPORTS INFLUENCE BEHAVIOR

So far, we have mainly focused on the relationship between gap distance and behavior, and discussed some reasons why different behaviors might be used at different distances. However, structural features of the supports forming a gap, as well as the animal's ability to make use of these features, may also have significant effects on the suitability of a given behavior. Three of the most critical features of arboreal supports include their orientation, shape, and stability (Cartmill, 1974), and we discuss the influence of these features on gap-crossing behavior in turn.

6.1 | Gap orientation

Animals may move across gaps in a variety of directions, and gap orientation may constrain behavior. More generally, substrate orientation has been found to influence locomotor behavior in a range of taxa, including primates (e.g., Hanna, 2006), snakes (e.g., Astley & Jayne, 2007), lizards (e.g., Spezzano & Jayne, 2004), and frogs (e.g., Herrel et al., 2013), as animals face challenges associated with moving against gravity. The case is likely to be similar with gap crossing, where the additional challenge of supporting the body mid-air becomes relevant. Because the torque experienced by a reaching animal depends on the angle between its movement pathway and the gravitational vector, animals moving more horizontally will need to exert greater effort to avoid buckling. However, as a path becomes more vertical, the animal must do more work against gravity, leading to different requirements for force production and balance.

Vertically downward trajectories, though, involve moving with rather than against gravity, and therefore, animals should be able to cross greater distances moving downward than in other directions. This hypothesis is supported in the case of snakes and jumping spiders. One species of jumping spider (*Phidippus regius*) can jump across the largest gaps when descending, followed by horizontal and ascending jumps (Nabawy et al., 2018). In addition, several snake species (*Boa constrictor*, *Boiga irregularis*, *Pantherophis guttatus*) also bridge the largest gaps when moving vertically downward, and experience better performance when ascending than when moving horizontally (Byrnes & Jayne, 2012; Hoefer & Jayne, 2013). To our knowledge, these differential challenges have only been explicitly tested in the brown tree snake. These snakes exhibit more muscular activity during horizontal gap crossings than they do during vertical crossings (Jorgensen & Jayne, 2017). They also exhibit intermediate activity during upward movements, likely associated with stabilization and mass movement (Jorgensen & Jayne, 2017).

Turning to the left or right while gap crossing (i.e., crossing with non-zero yaw angle), may also entail different challenges to relatively straight movements. Difficulties associated with yaw movements have been demonstrated in some snake species, which show a preference for trajectories with lower yaw angles, potentially due to the rolling torques that result from angled body positions (Hoefer & Jayne, 2013). These effects were smaller than those associated with verticality (Hoefer & Jayne, 2013), and may be less relevant for animals with a greater ability to turn their bodies to face angled targets. Investigations into when animals adjust body position on the origin support to reach angled targets, as opposed tochanging reaching angles or mid-gap behavior, would increase our understanding of the challenges associated with off-axis movement during gap crossing.

6.2 | Support shapes

The shape of the supports on which an animal moves is known to influence locomotor behavior in a range of taxa. One aspect of shape that has received significant attention is the diameter or width of the support substrate, which has been documented to influence locomotion in snakes (Astley & Jayne, 2007; Jayne et al., 2014; Jayne, Olberding, Athreya, & Riley, 2012), lizards (Herrel et al., 2013; Mattingly & Jayne, 2004; Spezzano & Jayne, 2004), tree frogs (Herrel et al., 2013), primates (Stevens, 2008), harvest mice (Karantanis et al., 2017), and opossums (Lammers & Biknevicius, 2004). Generally, small supports involve an increased risk of toppling, and many animals use different grasping behaviors or gaits on small supports to maintain balance (Biewener & Patek, 2018).

The relationship between locomotor performance and substrate diameter is variable. In some species, such as frogs and opossum, increasing diameter leads to faster locomotion, at least for some size ranges (Herrel et al., 2013; Lammers & Biknevicius, 2004). However, in white-footed mice (Hyams, Jayne, & Cameron, 2012) and snakes (Jayne & Herrmann, 2011), intermediate diameter branches lead to the fastest speeds, potentially due to challenges associated with gripping overly wide or overly narrow supports. Furthermore, diameter has minimal effects on jumping performance in lizards (Grabar, Gilman, & Irschick, 2016; Losos & Irschick, 1996), suggesting that substrate diameter can have different performance effects on different behaviors even within the same species.

The differential effects of diameter on performance may lead to preferences for some gap-crossing behaviors over others on thin origin branches. However, the shape of the target is also likely to influence gap-crossing performance and behavior. For example, brown tree snakes lunge more frequently toward wider targets and to targets with pegs, and never lunge toward vertical targets (Jayne et al., 2014). Additionally, tree frogs landing on narrow branches (width < body length) exhibit a range of landing behaviors that often involve a period of swinging below the target before the frog is able to stabilize itself (Bijma, Gorb, & Kleinteich, 2016). It seems likely that landing on narrow targets is difficult for both accurate targeting and regaining stability after the jump, but whether these results from snakes and frogs extend to a wider range of taxa and behaviors is unclear.

6.3 | Support compliance

The relationship between support compliance and jumping performance has received significant attention. Increased support compliance is often disadvantageous, as animals typically lose energy from their propulsive movements to the motion of the support. As such, a wide range of taxa, including click beetles (Ribak, Reingold, & Weihs, 2012), anoles (Gilman, Bartlett, Gillis, & Irschick, 2012), and some primates (Demes, Jungers, Gross, & Fleagle, 1995), experience decreased jumping performance on compliant surfaces.

However, some animals are able to minimize the costs associated with compliance. Cuban tree frogs, for example, are able to recover much of the energy lost to compliance by timing their jumps, although performance is still decreased relative to flat surfaces (Astley, Haruta, & Roberts, 2015). Gibbons also alter their jumping mechanics to counter the negative effects of compliance (Channon et al., 2011). How this effect translates to gap crossing has not been investigated, but it seems likely that the ability to tune behavior to compliance should influence the performance of dynamic crossing behaviors.

The compliance of target supports may also be relevant to gap-crossing ability. When landing on more compliant branches, diamond doves take longer to achieve stability, and require the use of balancing counter-movements more frequently (Crandell, Smith, Crino, & Tobalske, 2018). However, there are potential advantages of compliance; the tree-swaying of orangutans, for example, would not be possible without it (Chappell, Phillips, van Noordwijk, Mitra Setia, & Thorpe, 2015; Thorpe et al., 2007). Indeed, orangutans appear to be able to assess compliance, potentially using branch diameter as a proxy, and adjust locomotor behavior to match (Thorpe, Holder, & Crompton, 2009; van Casteren et al., 2013). In theory, substrate compliance could also be used as a power-amplifying mechanism (Ilton et al., 2018) to increase performance of impulsive behaviors, akin to a human jumping on a diving board. To better understand how compliance influences gap-crossing, further studies of movement on branches of known compliance would be of value (e.g., Hunt et al., 2017; Hunt, Jinn, Libby, Jacobs, & Full, 2014), particularly focusing on non-airborne or quasistatic behaviors.

7 | CONCLUSIONS AND SUGGESTIONS FOR FUTURE INVESTIGATION

The arboreal environment encompasses a complex system of supports and empty spaces (Dial et al., 2004), and canopy inhabitants must simultaneously respond to orientation, shape, and stability of branches as they move between supports. Animals moving across uneven terrain face similar challenges, with rocks and other three-dimensional features creating spannable spaces. The interplay of these ecological and mechanical factors makes the analysis of gap crossing a fascinating subject, and one deserving of further detailed analysis.

Once understood in the lab, the mechanical factors that influence gap-crossing behavior can be put into ecological context. Presumably, motivation influences behavioral choice as well as physical gap features. An animal escaping from a threat, for instance, may prioritize speed over landing control. Studies of animals crossing similar distances under different motivational paradigms would help address these hypotheses. Indeed, the factors that influence whether an animal chooses to cross a given gap at all, as opposed to navigating a new route, have not been fully elucidated. To fill in this information, long-term studies of animal movement in the field are required. Animal-borne data loggers may be one avenue for such research, if, for example, accelerometer patterns associated with gap crossing can be identified.

The importance of these details lies in part in the relationship between gap-crossing ability and other aspects of animal movement, particularly for animals in arboreal environments who face frequent gap-crossing challenges. Forest structure influences the energy landscape of the environment, and as such contributes to a range of evolutionary and ecological issues, including the diversity of primate species (Gouveia, Villalobos, Dobrovolski, Beltrão-Mendes, & Ferrari, 2014), the foraging strategy of birds (Whelan, 2001), and the movement patterns of a number of species (Manduell, Harrison, & Thorpe, 2012; McLean et al., 2016; Pringle, Webb, & Shine, 2003; Wells, Pfeiffer, Lakim, & Kalko, 2006). The challenges animals face when crossing gaps in the environment contribute to these relationships, and as such, understanding how animals solve these challenges can help us predict their movements, lend insight into management and conservation priorities, and allow us to better understand the evolutionary and ecological pressures associated with animal locomotion.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

AUTHOR CONTRIBUTIONS

M. G. and J. J. S. conceived the review. M. G. drafted the manuscript and made the figures. M. G. and J. J. S. edited the manuscript.

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