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Bear Locomotion



Sonia Amanat¹, Jonathan Mayer²,
Hashim Paracha², Zane Ali² and
Michael C. Granatosky³

¹New York Institute of Technology College of
Osteopathic Medicine, Old Westbury, NY, USA

²Department of Biology, New York Institute of
Technology, Old Westbury, NY, USA

³Department of Anatomy, New York Institute of
Technology, Old Westbury, NY, USA

fairly solitary lives with large home ranges. The need for these sizeable habitats requires bears to be highly adaptable and flexible in terms of diet and locomotor behavior. Bears range in diet from bamboo specialists to the largest land carnivores. In terms of locomotor modes, some species are highly arboreal while others utilize mixed aquatic and frozen tundra landscapes (Nowak 1999). This article discusses some of the general aspects of **bear locomotion**, while briefly touching on some of the more specialized locomotor behaviors observed in the family.

Synonyms

Bear gaits; Ursid locomotion

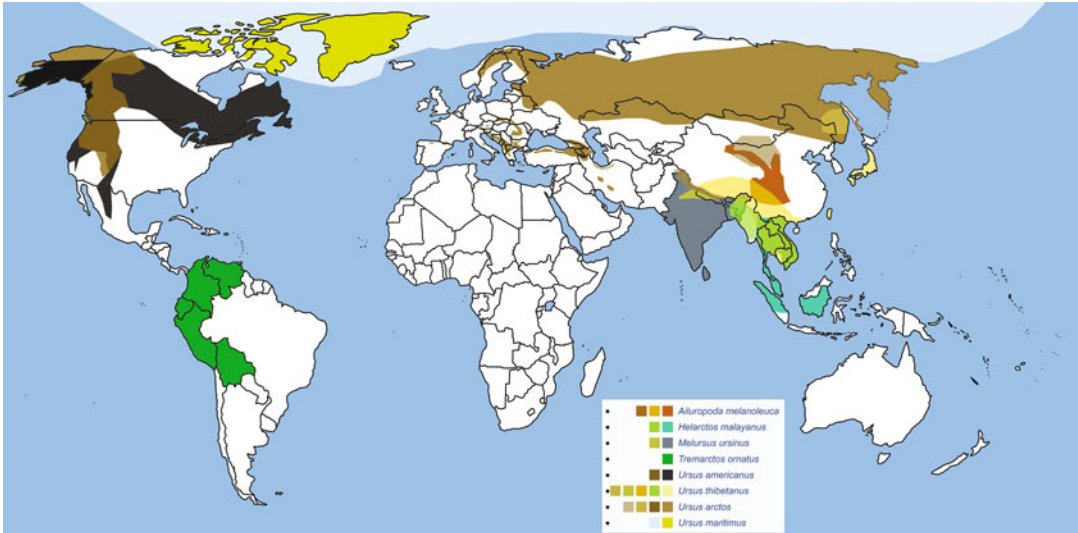
Definition

Movement used by members of the family Ursidae to traverse their environment.

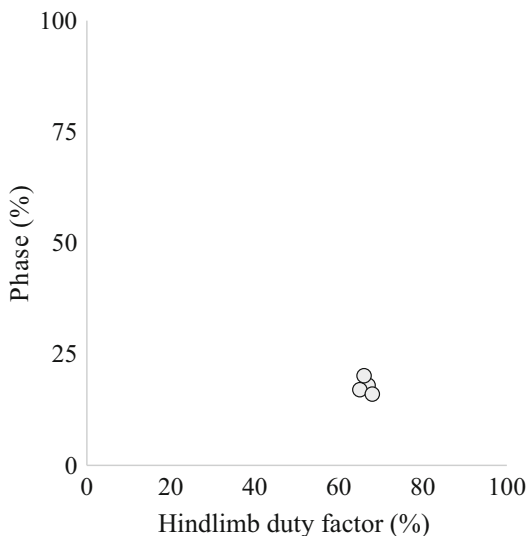
All bears belong to the family Ursidae. There are only eight recognized species of living bears, most belonging to the genus *Ursus*. Despite their limited taxonomic diversity, they have a near global range and can be found on all major landmasses except Antarctica, Africa, and Australia (Fig. 1). Members of the family come in various forms and sizes and range in body mass from the 68 kg sun bear (*Helarctos malayanus*) to the 700 kg polar bear (*Ursus maritimus*). Despite the range in body size and anatomy, all bears live

Bear Gaits and General Locomotor Behaviors

Bears' walking gaits consist of slow speed lateral-sequence lateral-couplet footfall patterns (Fig. 2). A lateral-sequence gait is one in which each hindlimb footfall is followed by an ipsilateral forelimb footfall (i.e., right hindlimb, right forelimb, left hindlimb, left forelimb). Commonly, during walking gaits, the forelimbs and hindlimbs are traveling together as a slightly asynchronous couplet. When the ipsilateral forelimbs and hindlimbs are traveling together, this is referred to as a lateral couplet; when the contralateral forelimbs and hindlimbs are traveling together, this is referred to as a diagonal couplet. Very rarely do the limbs move together in perfect synchrony. Lateral-sequence lateral-couplet footfall patterns tend to be present in long-legged terrestrial



Bear Locomotion, Fig. 1 Map demonstrating the current range of extant ursid species



Bear Locomotion, Fig. 2 “Hildebrand” plot displaying phase against hindlimb duty factor collected during quadrupedal walking in ursids ($n = 4$ species)

animals and are assumed to be the best mechanism in preventing interlimb interference. However, this footfall pattern is thought to be inherently unstable because a majority (~66%) of the stride is spent as a unilateral bipod (i.e., only two ipsilateral limbs in contact with the support), which tends to roll the body side-to-side throughout the stride. This instability is argued to be negligible

for long-legged animals (Granatosky 2018; Hildebrand 1976).

As locomotor speed increases, bears tend to change gait type. The gallop is the preferred means of locomotion when traveling at speeds more than 4 m s^{-1} . At intermediate speeds ($2\text{--}3 \text{ m s}^{-1}$), bears deviate from the usual mammalian pace or trot, and instead utilize a running walk, which is a footfall sequence consistent with their normal pattern of walking, but with decreased overlap between the feet. The trot and the pace require forelimbs and hindlimbs of equal length, with a straight short back; bears are characterized as having a relatively long, sloping back and this may limit their use of these gaits. One of the benefits of the running walk over a trot or a pace is the limited vertical fluctuation in the center of mass, as well as the ability to maintain contact with the ground with at least one foot throughout the stride. This suggests the apparent lack of a trot by grizzly bears may have implications for energetics as well. A lack of spring-like behavior in the bears’ wrists may also be a reason why they prefer a running walk gait. A trot is more efficient for animals that store elastic energy in their tendons. Due to the shorter overlap between steps in a running walk, it is less affected by the need for elastic energy storage (Shine et al. 2015).

As with most nonprimate mammals, the forelimbs of bears tend to support the majority of their body weight (approximately 54–60%) (Granatosky et al. 2018). At walking speeds, the limb loading forces seen in the hindlimb have a characteristic M-shape pattern, which is possibly due to limb stiffness (Shine et al. 2015). This pattern is not seen in the forelimbs and is likely due to differences in impulses and weight distribution. The hindlimbs also tend to have the greatest rate of force development except at fast locomotor speeds. In terms of fore-aft forces, the forelimbs tend to be net breaking across all speeds. The propulsive impulses of both the forelimbs and hindlimbs are very similar. Bears differ from other large mammals in having substantially higher forelimb and hindlimb mediolateral forces. Such ground reaction force patterns may be attributable to the lumbering and splayed postures of the limbs (Shine et al. 2015).

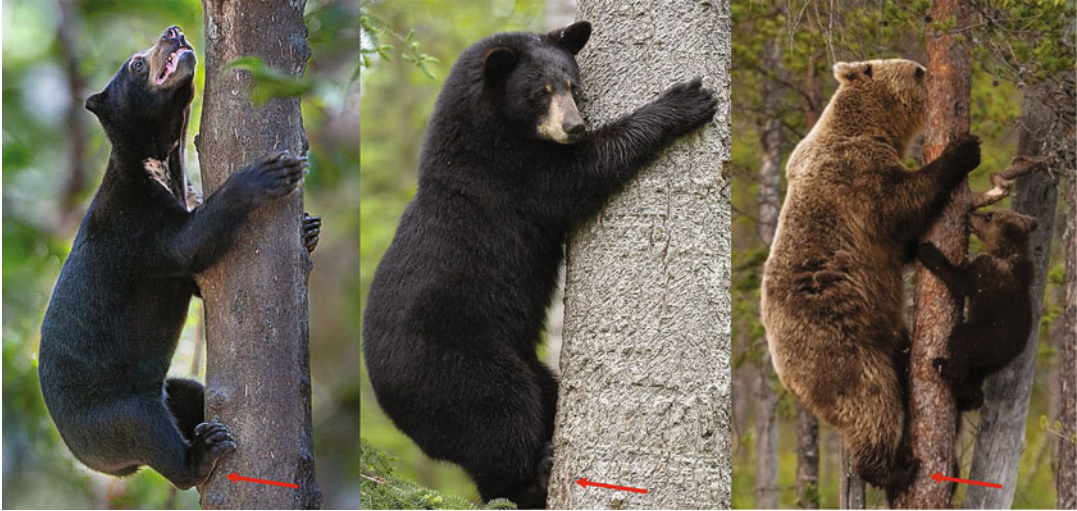
Plantigrade Locomotion

Foot postures are referred to as plantigrade when the complete length of the foot, involving the podials and metapodials, is positioned on the ground. This foot posture is observed in both bears and humans (Cunningham et al. 2010; Pagano et al. 2018). Some hypothesize that plantigrady infers energetic benefits as the larger contact area minimizes directional change of the center of mass trajectory, which in turn lessens mechanical energy loss (Cunningham et al. 2010). Pagano et al. (2018) tested this hypothesis in bears by collecting mass-specific energetic costs of locomotion in grizzly (*Ursus arctos*) and polar (*Ursus maritimus*) bears. At routine walking speeds, they observed that polar bears and grizzly bears exhibited similar costs of locomotion and gait kinematics. Minimum cost of transport while walking in both species was comparable to predictions for similarly sized quadrupedal mammals, but these costs doubled at higher speeds. Similar to humans, bears appear to exhibit a greater economy while moving at slow speeds. Despite walking costs that were similar to those of other quadrupedal mammals, Pagano et al.

(2018) found that both polar bears and grizzly bears have postural costs that are more than double predictions based on other quadrupedal mammals. The increased postural cost in both bears may in part be a result of their plantigrade posture as more erect limb postures (e.g., digitigrade and unguligrade) are known to have lower muscle mass and greater effective mechanical advantage (Biewener 1989; Reilly et al. 2007). Increased costs of running associated with plantigrade locomotion may also be attributable to the heel that absorbs energy once the stride begins. This eventually restricts storage and rehabilitation of elastic strain energy, mainly in the extensor muscles of the ankles.

Arboreal Locomotion

Arboreal movement remains an understudied aspect of the locomotor repertoire of bears. However, not all bear species are equally proficient. The Malayan sun bear (*Helarctos malayanus*) is largely arboreal and is known as the best tree climber within the Ursidae. The sun bear is characterized by strongly curved, pointed claws and large paws with naked soles, which make them well adapted for climbing trees. Additionally, this species is capable of supinating the ankle, allowing the hindfeet to “grip” the substrate rather than relying on claws or branches. In comparison, the larger brown bear shows little propensity for arboreal locomotion. These species are unable to “grasp” with the hindlimbs and instead keep the feet in a highly dorsiflexed position during vertical ascent (Fig. 3). Sasaki et al. (2005) demonstrated that these differences in relative climbing abilities have distinct consequences on the anatomy of the hindlimb. Specifically, they observed that the tarsal joint and foot of the sun bear and giant panda are more flexed and supinated than the polar bear and brown bear. Additionally, the tendon of the *m. tibialis cranialis*, a dorsiflexor and supinator of the foot, is shorter in the Malayan sun bear and the giant panda compared to other species. The combination of both traits allows the foot of arboreal bear species to be dynamically



Bear Locomotion, Fig. 3 Arboreal capabilities of the Malayan sun bear (*Helarctos malayanus*; left), black bear (*Ursus americanus*; middle), and grizzly bear (*Ursus*

arctos; right). Note the supinated versus dorsiflexed position of the ankle in the highly arboreal Malayan sun bear versus black and grizzly bears

fixed and stable to external forces while positioned in a supinated posture.

The black bear (*Ursus americanus*) is also quite adept at arboreal locomotion (Bull et al. 2000) and will quickly ascend into trees or other high places when feeling threatened. Often, bear-human interactions result in black bears refusing to leave trees. Such instances often require wildlife professionals to intervene and safely remove the bear from the tree (Wolfe et al. 2008) and relocate it to an area away from human interference.

Swimming

All North American bear species (i.e., black bears, brown bears, and polar bears) are all capable of swimming. Bears will take to the water for purposes of fishing or travel. In the water bears can reach swimming speeds upwards of 2.7 m/s. Swimming is most important for polar bears as they move between sea ice patches. Pagano et al. (2012) reported that the duration and distance of long-distance swimming ranged 0.7–9.7 days and 53.7–687.1 km in polar bear. They demonstrate that adult female polar bears and their cubs are capable of swimming long distances during

periods when extensive areas of open water are present. However, long-distance swimming appears to have higher energetic demands than moving over sea ice.

Griffen (2018) demonstrated that mean metabolic rate for a swimming polar bear to be $2.75 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$. When compared at the same movement rate, the cost of transport for swimming was estimated to be approximately $5 \times$ that of walking. These findings demonstrate that increasing frequency and duration of long-distance swims in polar bears is energetically stressful. Energetic and thermodynamic costs of long swims may be further exacerbated by recent declines in body condition that have been documented due to climate warming.

Captive Pacing Behavior

Species held captive in zoo like settings are often recognized for having particular behavioral abnormalities. Abnormal behavior in captive animals can include stereotypic behaviors – highly repetitive, invariant, functionless behavior, such as repetitive pacing, swaying, head-bobbing, bar-biting, over-grooming, or excessive licking. These behaviors can result from the frustration

of natural behavior patterns, impaired brain function, or repeated attempts to deal with some problem (Swaigood and Shepherdson 2005). For bears held captive, their daily activities include exploration and foraging but the bulk of it consists of pacing (40–60%). Pacing behavior is continuous walking back and forth or in a circle, following the same path. Signs of regular pacing include definite paths worn in the ground. Observational studies have explored pacing in depth and have confirmed a stereotypic pattern of pacing present in certain bear species and not others. The black bear, for example, shows a classic and stereotypic pacing behavior in contrast to sloth bears. The black bear paces up to 8 hours/day with increased rates before and after feeding time. Cless et al. (2015) proposed a quantitative definition of pacing based on a reduction of locomotor variability compared to other “directed locomotor tasks” in polar bears. Such a finding indicates that pacing may constitute a similar invariant repetitive behavior similar to patients with autism. However, Granatosky et al. (2020) note that locomotor rhythmicity is a normal component of bird and mammal locomotion independent of pacing behaviors. The factors that predispose bears to pacing in zoos may be linked to large home range size, large daily travel distance, or large body size (Mason and Clubb 2004).

Conclusion

As a group, the bears represent some of the largest living land carnivores. While they are limited in taxonomic diversity, they occupy a large geographic range. The quadrupedal gaits of bears are consistent, both metabolically and spatiotemporally, with other similarly sized mammals at slow speeds, but vary considerably when speed increases. Specifically, bears use running walks that are associated with increased costs of transport instead of trotting or pacing gaits. Limb loading for bears is distinct compared to other mammals due to relatively high mediolateral forces. These odd gait features may be attributable to plantigrade foot postures present across all bear species. Beyond terrestrial locomotion, some bear

species are quite proficient at arboreal movement. The propensity to locomote in the trees varies considerably across the living taxa and is largely driven by body size (i.e., smaller species are more arboreal) and the ability to supinate the ankle joint. As a consequence of either large home range size, large daily travel distance, or large body size, bears are especially prone to pacing behaviors in zoos. Research to curb such behavior is active and ongoing.

Cross-References

- ▶ [Adaptation](#)
- ▶ [Arboreality](#)
- ▶ [Canine Locomotion](#)
- ▶ [Evolution](#)
- ▶ [Mammalia](#)
- ▶ [Rainforest](#)
- ▶ [Semi-terrestrial](#)
- ▶ [Zoology](#)

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