

Gait characteristics of cheetahs (*Acinonyx jubatus*) and greyhounds (*Canis lupus familiaris*) running on curves

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Abstract. Turning ability is a factor that determines success in hunting prey and escaping from predators. However, little is understood about the biomechanics of turning at high speeds. We investigated gait characteristics of the cheetah and greyhound while running in a straight line and on curves. Four cheetahs and four greyhounds were filmed running around a 400-m track consisting of two 80-m straights and two bends with a radius of 38 m in a counterclockwise direction. The animals were motivated to run using a lure with speeds of 15–18 m s⁻¹. We found that the footfall order was fixed during curve running, although it was variable while running straight. Both the cheetahs and greyhounds used the rotatory gallop with the footfall order of right fore, left fore, left hind, and right hind during curve running. The duty factor increased on curves compared with straight running for three out of the four limbs in the greyhounds, but only for the inside hindlimb in the cheetahs. Interlimb coordination varied across running conditions in the cheetahs, but was unchanged in the greyhounds. The results suggest that animals do not use exactly the same strategies to deal with curve running.

Key words: duty factor, locomotion, maneuverability, rotatory gallop, turning.

Success in hunting prey and escaping from predators, which greatly affects fitness, depends on many factors. One factor is maximum speed. The faster animals run, the greater the possibility of successful hunting and escape is. Another factor is the ability to make a turn at high speeds. Prey species of cursorial carnivores often attempt to escape by abruptly changing directions just before they are caught up with by the predator (Alexander 2003). An experimental study using a tablet-based game that simulated predator-prey chases found that both speed and turning ability affected escape success (Clemente and Wilson 2016). Most studies on legged locomotion have focused on walking and running in a straight line at a steady speed. As turning ability is important for survival success, knowledge of the biomechanics of turning at high speeds helps us to further our understanding of form-function relationships in animals. To this end, we investigated gait characteristics of the cheetah (*Acinonyx jubatus*) and greyhound (*Canis lupus familiaris*) while

running in a straight line and on curves.

Interspecific comparisons present an opportunity to clarify whether strategies to deal with curve running differ between the cheetah and greyhound, both of which are characterized by superior sprinting ability. The cheetah is well known as the fastest land animal in the world and has morphological adaptations for high-speed locomotion (Russell and Bryant 2001; Hudson et al. 2011a, 2011b; Goto et al. 2013; West et al. 2013). In experimental conditions where food reward was used to encourage a cheetah to run in a straight line, the top speed was 29 m s⁻¹ (Sharp 1997). During hunting in the wild, the top speed of 25.9 m s⁻¹ was recorded (Wilson et al. 2013a). However, cheetah hunts are composed not only of maximum speed chases, but also of decelerating and turning with appropriate timing (Wilson et al. 2013b). The greyhound is one of the fastest dog breeds, and its hindlimbs are adapted for sprinting (Williams et al. 2008a, 2008b). The published running speed during

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a race was 16.45 m s^{-1} (Zebas et al. 1991). Straight running by the cheetah and greyhound has been examined in detail by Hudson et al. (2012) using high-speed video and force plate analysis.

At high speeds, the cheetah and greyhound use a form of gallop referred to as the rotatory gallop (Hildebrand 1959, 1977; Biancardi and Minetti 2012). In the rotatory gallop, landing and take-off are from ipsilateral limbs of each left-right pair. Specifically, the limbs make contact with the ground in the order of left fore, right fore, right hind, and left hind (clockwise) or right fore, left fore, left hind, and right hind (counterclockwise). The limb of a left-right pair that is the first to contact the ground is referred to as the non-lead limb or trailing limb. The contralateral limb is referred to as the lead limb. When animals gallop, they allocate biomechanical tasks unevenly among the limbs. In the rotatory gallop in the cheetah and greyhound at the speed of 18 m s^{-1} , the hindlimbs support a greater proportion of body weight than the forelimbs, with the non-lead and lead limbs contributing unequally to this task (Hudson et al. 2012).

The biomechanical demands of curve running differ from those of straight running. Animals running on curves must produce centripetal forces to change velocity heading in the new direction (Daley 2016). Several insights into the mechanics of curve running have been derived from experiments on humans. The maximum running speed on curves of differing radii (1–37.72 m) is slower compared with straight running (Chang and Kram 2007; Churchill et al. 2016; Taboga et al. 2016). In addition, the limb on the inside of the curve has a longer contact time and generates lower peak resultant ground reaction forces (GRFs) compared with the outside limb and the limbs during straight running (Chang and Kram 2007; Churchill et al. 2016). The factor that limits maximum curve-running speed is still controversial (Usherwood and Wilson 2006; Chang and Kram 2007; Churchill et al. 2016). However, lower peak resultant forces exerted by the inside limb indicate that the additional requirement to produce centripetal forces is not the sole limiting factor. Two studies have compared curve and straight running in the greyhound. Usherwood and Wilson (2005) reported that greyhounds did not slow down on curves compared with straight running. In contrast, Hayati et al. (2017) found that stride length was shorter during curve running with similar stride frequency between the two running conditions. As speed is the product of stride length and stride frequency, their results indicated slower speeds on curves. Further studies are needed to account for this

discrepancy.

In this study, we determined footfall patterns during straight and curve running in the cheetah and the greyhound. We then determined the duty factor, or relative limb contact time, for each limb. The duty factor is an important variable in studies of legged locomotion. This variable serves as a measure of the relative time allotted for reaccelerating and redirecting the center of mass of the body (Biknevicius and Reilly 2006). It was also used to predict the peak vertical GRF during equine locomotion (Witte et al. 2004). Finally, we evaluated interlimb coordination using the framework proposed by Abourachid (2003), which is explained in the following section, to discuss how much capacity animals have to change interlimb coordination to meet the changing demands of running.

Materials and methods

Four adult male cheetahs and four adult male greyhounds were the subjects in this study. These animals were housed at a zoo (Shanghai Wild Animal Park, China). The cheetahs were raised from infancy at the zoo. All experimental protocols were approved by the Institutional Animal Care and Use Committee at Yamaguchi University.

Experiments were conducted at the zoo. The cheetahs and greyhounds were encouraged to run around a 400-m track using a lure that travels ahead of them on the inside rail (Fig. 1A and B). The track was oval-shaped and composed of two 80-m straights that never cross connected by two bends with a radius of 38 m. The animals started from one corner between the bend and the straight, and ran the straight first and then the bend. The animals ran the track in a counterclockwise direction. The speed of the lure was controllable and set to $15\text{--}18 \text{ m s}^{-1}$. According to the study by Hudson et al. (2012), the cheetah and greyhound use a gallop at these high speeds. Video recordings were made using eight high-speed cameras: two MEMRECAM HX-7 cameras (nac Image Technology, Tokyo, Japan) and six EX-F1 cameras (CASIO, Tokyo, Japan). The cameras filmed the animals from a lateral or diagonal view with a frame-rate of 1000 or 1200 frames s^{-1} .

We analyzed gait characteristics in 47 straight-running strides and 37 curve-running strides of the cheetahs, and in 19 straight-running strides and 22 curve-running strides of the greyhounds. The stride period was defined as the time elapsed between two consecutive touchdowns of the non-lead forelimb. The time of touchdown and liftoff of

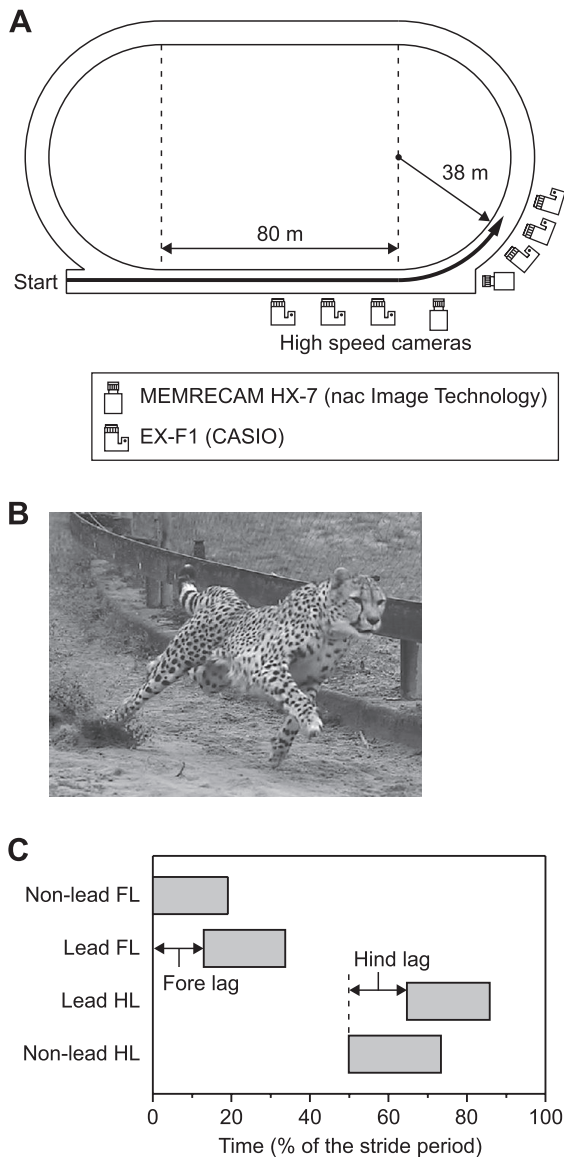


Fig. 1. A: A diagram of the track at Shanghai Wild Animal Park and the placement of eight high-speed cameras. The length of the track was 400 m. The two straight parts were each 80 m long, and the radius of the semicircular parts was 38 m. B: Photograph of a cheetah running on a curve. C: An exemplary gait diagram of the rotatory gallop. The stride period was defined as the time elapsed between two consecutive touchdowns of the non-lead forelimb and normalized to 100%. Horizontal grey bars represent the stance period. The fore lag was defined as the time between the touchdowns of the non-lead and lead forelimbs, and the hind lag was defined as the time between the touchdowns of the non-lead and lead hindlimbs. FL, forelimb; HL, hindlimb.

each limb during a stride were determined. The duty factor was calculated as the stance period relative to the stride period. In addition, the fore lag and hind lag were measured (Fig. 1C). These temporal parameters were proposed by Abourachid to quantify interlimb coordination and identify quadrupedal gaits (Abourachid 2003; Abourachid et al. 2007). The fore lag was defined as the

time between the touchdowns of the non-lead and lead forelimbs, and the hind lag was defined as the time between the touchdowns of the non-lead and lead hindlimbs.

All statistical tests were performed using OriginPro 2017 (LightStone, Tokyo, Japan). We could not identify the animals recorded in video clips individually because they were similar in appearance. Thus, the Student's unpaired *t* test was used to evaluate differences between straight and curve running for each limb within a species. The level of significance was set at $\alpha = 0.05$. Data are presented as the mean \pm *SD*.

Results

In all strides analyzed, the cheetahs and the greyhounds used the rotatory gallop (Figs. 2A and 3), and the order of footfalls was variable during straight running and was constant during curve running. During straight running in the cheetahs, the footfall order of the rotatory gallop was clockwise in 21 strides and counterclockwise in 26 strides. During curve running in a counterclockwise direction, the footfall order was always counterclockwise (Fig. 2B). In this order, the non-lead forelimb was the right forelimb, and the non-lead hindlimb was the left hindlimb. During the curve-running task used in this study, the right limbs were on the outside and the left limbs were on the inside of the curve. Similarly, during curve running in the greyhounds, the footfall order of the rotatory gallop was invariably counterclockwise.

The effects of curves on the duty factor of an individual limb differed between the two species (Table 1). In the cheetahs, the duty factor of the non-lead and lead forelimbs, and the lead hindlimb did not significantly change during curve running compared with straight running. However, the duty factor of the non-lead hindlimb was significantly greater during curve running. In the greyhounds, the duty factor of the non-lead hindlimb did not significantly differ between the two running conditions. The duty factor of both forelimbs was significantly greater during curve running. The duty factor of the lead hindlimb was greater during curve running, although the difference was not significant ($P = 0.055$).

The effects of curves on interlimb coordination also varied between the cheetah and greyhound (Table 2). In the cheetahs, the fore lag did not significantly differ between straight and curve running. However, the hind lag was significantly longer during curve running. In the greyhounds, the fore and hind lags did not significantly differ between the two running conditions.

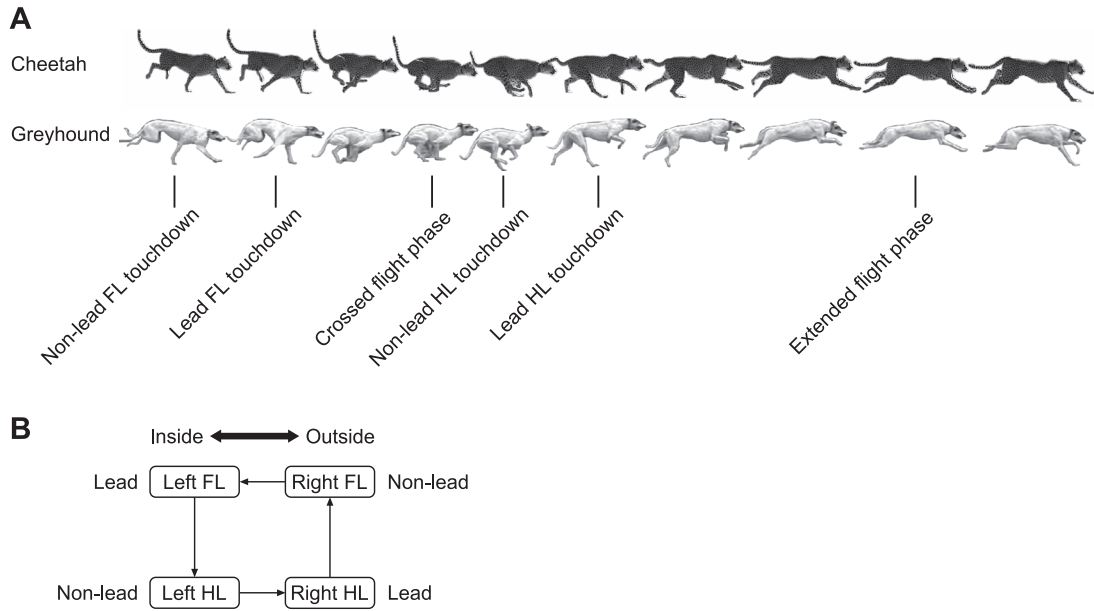


Fig. 2. A: The key points of the rotatory gallop in the cheetah and greyhound. B: The footfall pattern while running on curves in a counterclockwise direction. FL, forelimb; HL, hindlimb.

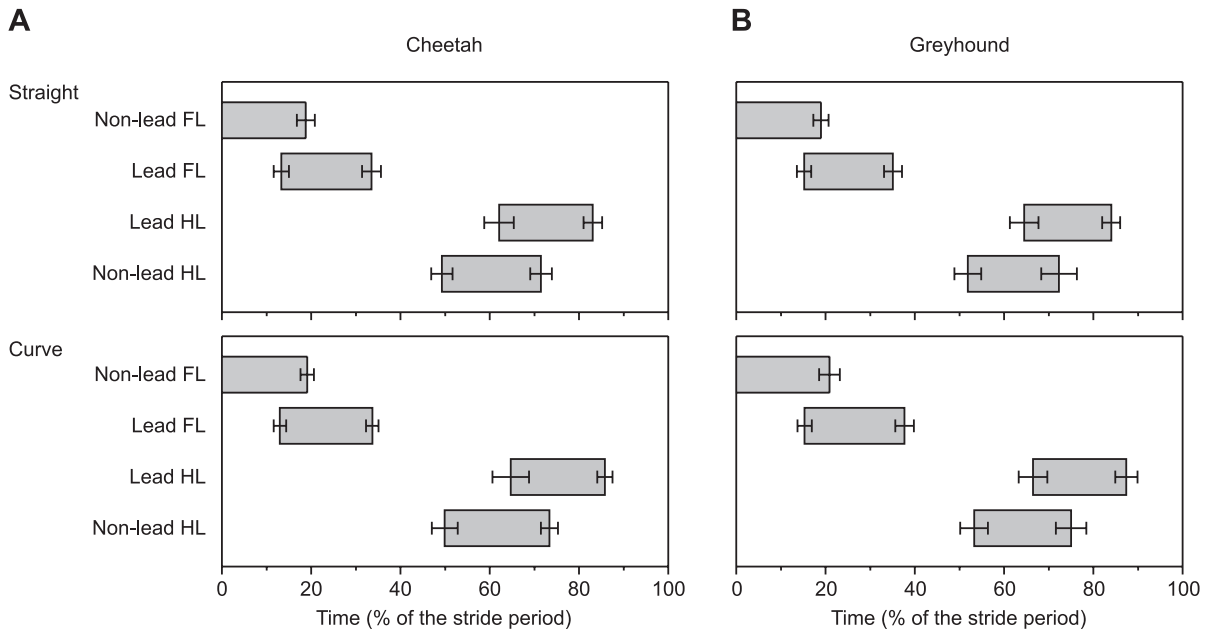


Fig. 3. Gait diagrams of straight and curve running in the cheetah (A) and greyhound (B). The stride period was normalized to 100%. Horizontal grey bars represent the mean \pm SD stance period for each limb. FL, forelimb; HL, hindlimb.

Discussion

We report three major findings. Firstly, the footfall order was fixed during curve running, although it was variable while running straight. Both the cheetah and greyhound used a rotatory gallop with a counterclockwise footfall pattern in all curve-running strides analyzed,

while running the track counterclockwise. Secondly, the duty factor increased on curves compared with straight running only for the non-lead hindlimb in the cheetah, but for three out of the four limbs in the greyhound (Table 1). As the animals ran the track in a counterclockwise direction, the non-lead hindlimb was the left limb on the inside of the curve. Lastly, the coordination between the non-

Table 1. The duty factor for each limb, expressed as a percentage of the stride period

Animal	Running condition	No. of strides analyzed	Limb			
			Non-lead fore	Lead fore	Non-lead hind	Lead hind
Cheetah	Straight ^a	47	18.8 ± 2.0	20.2 ± 2.1	22.2 ± 2.4	21.0 ± 2.1
	Curve ^a	37	19.1 ± 1.5	20.7 ± 1.4	23.5 ± 1.9	21.1 ± 1.7
	Percentage-point difference (curve minus straight)		0.3	0.5	1.3	0.1
	<i>P</i> value ^b		0.432	0.151	0.014	0.848
Greyhound	Straight ^a	19	19.0 ± 1.7	19.9 ± 2.0	20.4 ± 4.0	19.5 ± 2.0
	Curve ^a	22	20.9 ± 2.3	22.4 ± 2.1	21.7 ± 3.4	20.9 ± 2.5
	Percentage-point difference (curve minus straight)		1.9	2.5	1.3	1.4
	<i>P</i> value ^b		0.004	< 0.001	0.274	0.055

^a Values are means ± *SD*.

^b Differences between straight and curve running were evaluated using the Student's unpaired *t* test. Bold *P*-values indicate significance.

Table 2. Temporal parameters that quantify interlimb coordination, expressed as a percentage of the stride period

Animal	Running condition	Fore lag	Hind lag
Cheetah	Straight ^a	13.3 ± 1.7	12.8 ± 1.7
	Curve ^a	13.0 ± 1.4	14.8 ± 2.0
	Percentage-point difference (curve minus straight)	-0.3	2.0
	<i>P</i> value ^b	0.433	< 0.001
Greyhound	Straight ^a	15.2 ± 1.6	12.6 ± 1.8
	Curve ^a	15.3 ± 1.6	13.1 ± 1.7
	Percentage-point difference (curve minus straight)	0.1	0.5
	<i>P</i> value ^b	0.876	0.361

^a Values are means ± *SD*.

^b Differences between straight and curve running were evaluated using the Student's unpaired *t* test. Bold *P*-values indicate significance.

lead and lead hindlimbs changed with different running conditions in the cheetah, whereas interlimb coordination did not change significantly in the greyhound (Table 2). Furthermore, it is important to note two limitations of this study. Firstly, our study did not measure the running speed of the animals for each stride. This limitation does not allow us to discuss interspecific differences in curve-running performance as defined by maximum curve-running speed relative to maximum straight-running speed. Secondly, we could not identify the animals recorded in video clips individually. As a result, we pooled data from different individuals of the same species, used the Student's unpaired *t* test to evaluate differ-

ences between running conditions, and do not discuss the inter-individual variation in the duty factor and interlimb coordination.

This study demonstrates that both the cheetah and greyhound fix the rotatory gallop footfall order during curve running using a counterclockwise sequence of footfalls, in the order of right fore, left fore, left hind, right hind, when running the track in a counterclockwise direction. This finding is in agreement with Hildebrand's (1977) findings, which showed that the inside forelimb was used as the lead limb when turning. A preference for one footfall order during curve running is also observed in horses, which use a transverse gallop rather than the rotatory gallop. Horses show a preference for the inside limb as the lead limb despite the direction of the curve (Hildebrand 1980; Williams and Norris 2007; Barrey 2013). Thus, the use of the inside forelimb as the lead forelimb is common in both rotatory and transverse galloping. It is believed that horses maintain balance more easily on the inside lead than the outside lead (Hildebrand 1980; Barrey 2013). Similar factors may affect the choice of footfall order in the cheetah and greyhound. It is of interest to investigate whether the cheetah and greyhound use the clockwise footfall sequence on curves when running a track in a clockwise direction. However, to the best of our knowledge, no one has provided a mechanical explanation for why the inside lead of the forelimb improves balance on curves. In both forms of gallop, the lead forelimb is the last limb to leave the ground before the crossed flight phase when animals cannot generate GRF (Fig. 2A; Bertram and Gutmann 2009; Biancardi and

Minetti 2012). Therefore, the inside lead of the forelimb may be related to fine adjustments of speed and direction during the crossed flight phase.

Two studies reported the duty factor during high-speed running in the cheetah and/or greyhound. Hudson et al. (2012) presented a graph showing the duty factor for the non-lead forelimb during straight running in the cheetah and the greyhound. Within the range of speeds covered in this study (15–18 m s⁻¹), the results of Hudson et al. (2012) and our results show similar values. This concordance supports the validity of our measurements. On the other hand, the duty factor in the greyhound reported by Usherwood and Wilson (2005) is generally smaller than that in our study despite the similar speeds. Some differences in methodology exist across studies. The camera frame rate was 250 frames s⁻¹ in the study by Usherwood and Wilson (2005). We used high-speed cameras that enabled a finer time resolution, at 1000 or 1200 frames s⁻¹. The radius of the track used by Usherwood and Wilson (2005) was 22.4 m, but was 38 m in this study.

The percentage-point differences (up to 2.5 percentage points) in the duty factor and hind lag between running conditions may seem trivial (Tables 1 and 2). However, only a short time is available during high-speed locomotion to change speed and direction. For greyhounds running straight at speeds of 15.19–16.33 m s⁻¹, the stride period is 283.7–292.4 ms, and the contact time of individual limbs in a stride is 40.2–50.8 ms (Usherwood and Wilson 2005). Stuart et al. (1973) showed that a large change in the galloping speed (from 4.63 to 5.82 m s⁻¹) of a cat on a treadmill was related to a relatively small change in absolute and relative limb contact time. Therefore, the observed differences between running conditions in this study are worth considering.

The interspecific differences in the effects of curves on the duty factor and interlimb coordination suggest that the cheetah and greyhound use different strategies to deal with curve running. Animals running on curves continuously change velocity heading in the intended direction of travel. The results from previous experiments on humans suggested functional differences in the role of the limbs during curve running. Churchill et al. (2016) demonstrated that the inside limb, which had a longer contact time, generated greater peak inward GRF and net inward impulse than the outside limb during human curve-running. They argued that the inside limb was used primarily for generating centripetal forces, and the outside limb was used primarily for propulsion and weight support. Our study showed that the cheetah increased the

duty factor only for the inside, non-lead hindlimb during curve running (Table 1). Although we did not perform GRF measurements to assess functional differences in the role of the limbs, we consider the inside, non-lead hindlimb of the cheetah to play a greater role in producing centripetal forces, and thus changing velocity heading. The other three limbs may play a role mainly in maintaining speed. The greyhound increased the duty factor for the non-lead and lead forelimbs and the lead hindlimb, suggesting that more limbs place more emphasis on changing direction rather than maintaining speed compared with cheetahs. The significant change in the hind lag between running conditions suggests that the cheetah has a greater ability to move each hindlimb individually than the greyhound. In contrast, the fore lag did not change in either species, suggesting a similar ability to move each forelimb individually.

The strategies used to deal with curve running by the cheetah may be advantageous for two reasons. Firstly, increasing the hindlimb duty factor may be more efficient than increasing forelimb duty factor because the hindlimbs support a greater proportion of body weight than the forelimbs during high-speed running (Hudson et al. 2012). Supporting more body weight on the hindlimbs enhances grip and reduces the risk of slipping (Hudson et al. 2012). Secondly, the inside limbs may be more tilted than the outside limbs during curve running, and thereby efficient at producing centripetal forces. During curve running, animals lean their body towards the center of the curve (Usherwood and Wilson 2005; Brocklehurst et al. 2014). As a result, the proximal joint, shoulder or hip of the inside limb is located lower than that of the outside limb. This asymmetry in the limb position may cause the differences in the coronal plane angle between the limb and the ground during stance, and thus in the effectiveness of producing centripetal and propulsive forces. The cheetah's ability to move each hindlimb individually may contribute to differing use of the inside and outside hindlimbs. Future studies are required to perform kinetic and kinematic measurements that clarify the functional roles of each limb.

In summary, our results suggest that animals do not use exactly the same strategies to deal with curve running, although the effects of inter-individual variability on results need to be assessed in the future. The cheetah may assign the roles of changing velocity and heading in the intended direction of travel to the inside, non-lead hindlimb to a greater degree than to other limbs, while the greyhound may assign these roles to multiple limbs. We

expect future studies to clarify whether strategies to deal with curve running are associated with curve-running performance. This study extends our knowledge of non-steady locomotor behavior (Biewener and Daley 2007; Daley 2016). Although most studies have restricted measurements of locomotion on a level surface in a straight line at a steady speed, animals exhibit more complex behavior in their natural environment. Turning capacity and the ability to accelerate and decelerate rapidly are as important as maximum straight-running speed for hunting success in the cheetah (Wilson et al. 2013a, 2013b). Advances in inertial measurement and data-logging technology have enabled the collection of detailed locomotion data on free-ranging animals. Experimental studies based on such free-ranging locomotion data will give us a better understanding of different ecologically important aspects of locomotor performance in animals.

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