ZOOLOGY

The search for stability on narrow supports: an experimental study in cats and dogs

Eloy Gálvez-López [a,*], Ludovic D. Maes [b], Anick Abourachid [b]

[a] Department of Animal Biology, University of Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain
[b] Département Ecologie et Gestion de la Biodiversité, Muséum National d'Histoire Naturelle, MNHN USM 301, CNRS UMR 7179, Pavillon d'Anatomie Comparée, CP 55, 57 rue Cuvier, 75231 Paris cedex 05, France

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ABSTRACT

Kinematic and coordination variables were studied in two carnivorans, one with known locomotor capabilities in arboreal substrates (cat), and the other a completely terrestrial species (dog). Two horizontal substrates were used: a flat trackway on the ground (overground locomotion) and an elevated and narrow runway (narrow-support locomotion). Despite their different degree of familiarity with the 'arboreal' situation, both species developed a strategy to adapt to narrow supports. The strategy of cats was based on using slower speeds, coupled with modifications to swing phase duration, to keep balance on narrow supports. The strategy of dogs relied on high speeds to gain in dynamic stability, and they increased cycle frequency by reducing swing phase duration. Furthermore, dogs showed a high variability in limb coordination, although a tendency to canter-like coordination was observed, and also avoided whole-body aerial phases. In different ways, both strategies suggested a reduction of peak vertical forces, and hence a reduction of the vertical oscillations of the centre of mass. Finally, lateral oscillation was reduced by the use of a crouched posture.

1. Introduction

The gaits employed by animals when walking or running overground, and their corresponding dynamics and kinematics, have been rigorously studied since the 19th century (e.g., Marey, 1873; Muybridge, 1899; Manter, 1938; Hildebrand, 1966, 1980, 1985; Demes et al., 1994; Lee et al., 1999; Larson et al., 2000; Cartmill et al., 2002; Fischer et al., 2002; Abourachid, 2003; Hutchinson et al., 2006; Maes et al., 2008). Nevertheless, the ground is not the only support on which animals move; they also move on branches high in the forest canopy or dig their way through the ground. Each substrate requires different anatomical, morphological, and mechanical adaptations, as well as modifications to the dynamics and kinematics of locomotion (Biewener, 2003).

Locomotion on arboreal substrates has not been as thoroughly studied as overground locomotion, but its main particularities have already been covered (Cartmill, 1974, 1985; Meldrum, 1991; Schmitt, 1999, 2003a; Schmitt and Lemelin, 2002; Lemelin et al., 2003; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). The main problem affecting arboreal locomotion is the tendency of animals to roll (rotate around their sagittal axis) and topple from the support because all their support points are effectively collinear,

which greatly reduces their support polygon. Several solutions to this problem, each involving different morphological adaptations, have been described (Cartmill, 1985): (i) relatively short limbs, as in arboreal viverrids (Taylor, 1970), or the use of a crouched posture (Schmidt and Fischer, 2010), keep the body's centre of mass close to the support and minimise lateral oscillation; (ii) prehensile hands and/or feet allow gripping the branch and thus exerting a torque that resists the toppling moment, as in primates (Rollinson and Martin, 1981; Vilensky and Larson, 1989; Schmitt, 1999), some opossums (Schmitt and Lemelin, 2002; Lemelin et al., 2003), and tupaiids (Sargis, 2001); (iii) the reduced body size of small animals, like squirrels, overcomes the toppling problem by spreading the support points relatively more widely on the surface of the branch; and (iv) a foolproof solution to totally avoid toppling is hanging underneath the branch, like sloths do. Another source of locomotor instability during arboreal locomotion is the round section of branches, which increases the potential of slipping off them. Animals with prehensile hands and/or feet avoid this problem by firmly grasping the support; while clawed animals, whose grasping abilities are reduced or absent, change limb placement during arboreal locomotion to reorient substrate reaction forces inwards to the branch, and thus prevent slipping off it (Schmitt, 2003a; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). Finally, another problem affecting arboreal locomotion are vertical oscillations of the support. Branches, especially the fine ones, tend to deflect under an animal's weight, which not only hinders joint stabilisation, but

* Corresponding author.
E-mail address: egalvez@ub.edu (E. Gálvez-López).

might also toss the animal from the support due to elastic recovery. Schmitt (1999) proposed that animals use compliant gaits as a solution to this problem. Compliant gaits are characterised by substantial limb yield, which reduces vertical oscillations of the body (and thus of the support) and encourages long contact times, which in turn allows the reduction of stride frequency (and thus the potential of branch sway). Furthermore, compliant gaits reduce bone and joint stresses associated with flexed-limb gaits (Schmitt, 1999). The use of compliant gaits in primates, marsupials and other arboreal mammals was later confirmed by Larney and Larson (2004). In addition to compliant gaits, the use of a crouched posture has also been proposed as a mechanism to reduce vertical oscillations of the body both in compliant (Schmitt, 1999) and stiff gaits (i.e., when limb yield is low; Bishop et al., 2008). For the latter case, the authors proposed that, if limb protraction and angular excursion remained unaltered, the use of a crouched posture would reduce vertical displacement of the centre of mass by creating a smaller pendulum (and thus reducing potential energy fluctuations; Bishop et al., 2008). Finally, at higher speeds, ambling gaits have also been proposed as a solution to reduce vertical oscillations of the support, since they allow animals to maintain at least one foot in contact with the substrate during a stride, thus reducing peak vertical forces on the support (Schmitt et al., 2006).

Most studies on arboreal locomotion, though, focus on primates and, to a lesser extent, on some didelphids, since they consider these groups arboreal specialists, which present a set of adaptations to moving and foraging in an arboreal setting so marked that it makes their terrestrial locomotion distinct from that of other animals. These adaptations involve prehensile extremities, showing more protracted arm postures at touch-down, producing lower peak vertical substrate reaction forces with the forelimbs than with the hindlimbs, and using diagonal-sequence gaits almost exclusively when walking on narrow supports (Hildebrand, 1967; Vilensky and Larson, 1989; Demes et al., 1994; Larson et al., 2000; Schmitt and Lemelin, 2002). Nevertheless, arboreal specialists are not the only animals known to use arboreal substrates. As stated by Lammers and Biknevicius (2004), many small mammals use fallen logs and branches on the forest floor as arboreal runways. Furthermore, many terrestrial species often climb trees to escape predators or while hunting (MacDonald, 1984; Wilson and Mittermeier, 2009). Since stability in locomotion is directly linked to performance in escaping or hunting behaviours, and thus directly linked to fitness, it would be vital for these terrestrial mammals navigating arboreal substrates (non-arboreal specialists) to adapt their locomotion and increase their stability.

To date, locomotion on arboreal supports in non-arboreal specialists has only been studied in small species: the common marmoset (Callithrix jaccus) (Schmitt, 2003b), the grey short-tailed opossum (Monodelphis domestica) (Lammers and Biknevicius, 2004), and the rat (Rattus norvegicus) (Schmidt and Fischer, 2010). To increase their stability on arboreal supports, these animals reduced peak vertical forces to reduce the vertical oscillation of the centre of mass. Both the common marmoset and the rat used similar speeds and had similar contact times (i.e., duty factor, and thus stance phase duration) in overground and arboreal locomotion, while the grey short-tailed opossum used lower speeds and had longer contact times during arboreal locomotion. Schmidt and Fischer (2010) proposed that the reduction of speed could only be accomplished if some grasping ability is retained.

In the light of these results, we wonder how a larger non-arboreal specialist (for instance, a ground-dwelling carnivoran pursuing its prey up into the forest canopy) will adapt its kinematics and coordination to the arboreal substrate. Will larger mammals use the same strategy as the smaller ones? The first aim of this study was thus to determine how a medium-sized non-arboreal specialist adjusts its kinematics and coordination to adapt to an arboreal

substrate. For our experiments, we chose the domestic cat (Felis silvestris catus), which is accustomed to moving comfortably along branches, rails, and similar narrow, elevated supports. Taking into account the possible solutions for increasing stability presented above, cats were expected to increase stance phase duration, and thus decrease stride frequency. Slower speeds on narrow supports than on flat ground, as was found for the grey short-tailed opossum (Lammers and Biknevicius, 2004), were also expected, since cats can use their claws to grip the support. We also expected that they would display a more crouched posture in the 'arboreal' situation to bring the centre of mass closer to the support.

Secondly, we wondered whether the strategy employed by non-arboreal specialists to adapt to the arboreal situation, if there was any, would be a universal solution for all terrestrial species. That is, if we encouraged a completely terrestrial species into an arboreal-like situation, would it arrive at the same solution to keep balance and advance on the narrow support? To answer this question, we used a protocol similar to the one used for cats to study the kinematics and coordination of the domestic dog (Canis lupus familiaris) when moving along a narrow, elevated support, before comparing both strategies. We chose the dog because it is a completely terrestrial species whose kinematics and coordination overground have already been thoroughly studied (Hildebrand, 1968; Lee et al., 1999; Maes et al., 2008).

2. Materials and methods

All animals were healthy specimens, with no known pathologies that might affect their vision, balance, or locomotion. Due to the different degree of familiarity of the studied species with the arboreal situation, different experimental settings were used for each species. This way, animals were able to move along the support, but were at the same time forced to search for stability.

2.1. Cats

Seven cats (age = 5.9 ± 3.5 years; shoulder height = 0.27 ± 0.02 m; body mass = 4.4 ± 0.7 kg) were filmed on the ground and in an 'arboreal' situation (narrow-support locomotion). In overground locomotion, the cats moved along an 8 m flat carpet (Fig. 1A), while the arboreal situation was simulated by a wooden bar (0.03 m $\times$ 0.03 m $\times$ 2.50 m) raised to a height of 0.75 m (Fig. 1B). The trestles raising the wooden bar also prevented it from deflecting under the cats' weight, thus avoiding external
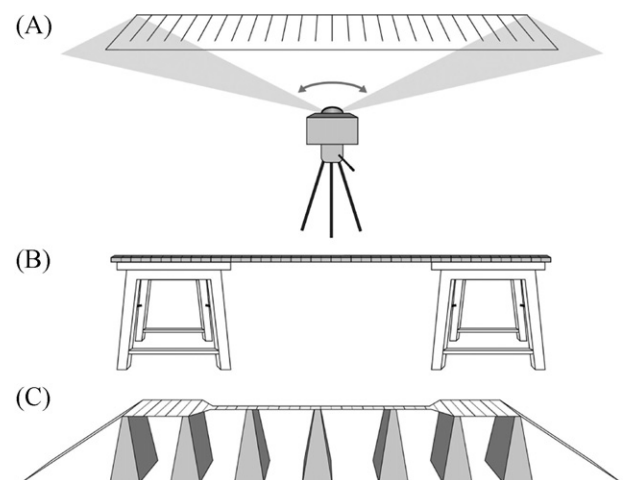

Fig. 1. Experimental situations for the comparison between (A) overground and (B and C) narrow-support locomotion for cats (B) and dogs (C). See text for details.

perturbations to their stability (e.g., induced vertical oscillations of the centre of mass). Black lines, perpendicular to the axis of locomotion, were painted at 0.05 m intervals both on the carpet and on the wooden bar and used to assess the location of each foot at touch-down (accuracy: 0.02 m). In both cases, the cats were placed at one end of the structure (bar or carpet) and were encouraged to go to the other end of it. A high-speed video camera (Basler A504K; Basler Electric Co., Highland, IL, USA), placed perpendicular to the trackway, 3.0 m from its centre (field: 1.0 m; resolution: 1280 pixels/m), was used to film the cats at a frequency of 125 Hz.

We are aware that the experimental situation that we used to represent arboreal locomotion is just an approximation, given that we used a narrow, square surface to simulate a support that tends to be round in section. Nevertheless, support width was approximately the same as feet width, which would probably affect stability to a similar degree as a round support of approximately half the body width of the animal. Although this last methodology is useful for studies dealing with changes in the orientation of ground reaction forces on arboreal settings (e.g., Lammers and Biknevicius, 2004), the former provides better insight on the effect of collinear limb placement.

2.2. Dogs

Five Belgian Shepherd dogs (age = 7.3 ± 1.7 years; shoulder height = 0.61 ± 0.04 m; body mass = 28.0 ± 5.0 kg) were filmed in an 'arboreal' situation. A 9 m long runway raised to a height of 1.5 m was used in this experimental situation. The elevated runway included a central narrow part (0.15 m × 5.0 m) simulating the arboreal situation, and two wide parts (0.5 m × 2.0 m) allowing the dog to stabilise prior to and after the narrow part (Fig. 1C). The whole structure was reinforced with small beams between the supports to avoid its deflection under the weight of the dogs, which would introduce external perturbations to their stability. Furthermore, since we were interested in the effect of support width, not support slipperiness, the whole surface of the runway was covered with a mix of paint and sand as an anti-slip coat. Black lines, perpendicular to the axis of locomotion, were painted on the runway at 0.10 m intervals and used to assess the location of each foot at touch-down (accuracy: 0.05 m). Since the dogs were trained for agility contests, they moved along the runway when asked by their owners. A high-speed video camera (Basler A504K), placed perpendicular to the runway, 10.0 m from its centre and at a height of 2.5 m (field: 2.0 m; resolution: 640 pixels/m), was used to film the dogs at a frequency of 125 Hz.

In the case of dogs, support width was about one and a half times the width of their feet, since dogs refused to perform the exercise on supports narrower than 15 cm. Nevertheless, this situation is comparable to the potential 'arboreal' situations that terrestrial mammals may face (e.g., a fallen log traversing a gap). Finally, given that the aim of this study was to search for possible modifications to kinematic and coordination variables of locomotion when comparing the 'arboreal' and the usual (overground) situation, we needed a minimum degree of regularity, which would not have been achievable if the animals had advanced on a truly arboreal substrate.

For overground locomotion, we revisited the data from a previous study that comprised all gaits of Belgian Shepherd dogs analysed in the anteroposterior sequence (APS) framework (Maes et al., 2008). Comparison between our data in the 'arboreal' situation and overground locomotion data from Maes et al. (2008) was possible because we used the same dog breed (Belgian Shepherds), and because the experimental procedure was based on the same processes.

2.3. Video analysis and data processing

All locomotor analyses in this study were carried out in the framework of the APS approach, since it allows the study of all kinds of interlimb coordination – symmetrical or asymmetrical gaits and unsteady locomotion – with the same set of variables (Abourachid, 2003; Abourachid et al., 2007; Maes et al., 2008). The APS method has already been described elsewhere (Maes et al., 2008, p. 140), and will only be briefly summarized here. The records were analysed using Virtual Dub (version 1.6.12; http://www.virtualdub.org/). The timings of touch-down (when the foot makes contact with the ground) and lift-off (when the last toe leaves the ground) of each limb were noted using frame number. A maximal error of one frame (i.e., 8.0 ms) was estimated for touch-down and lift-off timings. The positions of the feet on each touch-down were determined using the black lines marked on all experimental supports. The data were visualised using classical gait diagrams (Marey, 1873) and track diagrams (Abourachid et al., 2007), which allowed us to spot APSs and to manually identify gaits.

After video analysis, in each APS the following kinematic variables were calculated for the first forelimb to contact the ground (referred to hereafter as reference limb): cycle duration (D; in seconds), corresponding to the time between consecutive footfalls of the same foot; cycle frequency ($F = 1/D$; Hz); stance (St; s) and swing (Sw; s) phase duration, corresponding to the time that the foot is in contact with the ground, and the time that it is lifted, respectively, during each cycle; and stride length (L; m), corresponding to the distance between consecutive footprints of the same foot. Speed (u; m/s) was calculated using stride length and cycle duration ($u = L/D$).

We also calculated the following temporal coordination variables: fore lag (FL; %) and hind lag (HL; %), corresponding to the time between the footfalls of both limbs of a pair, fore and hind limb, respectively, in relation to the cycle duration of the reference limb; and pair lag (PL; %), corresponding to the time between footfalls of the first limb of each pair to contact the ground in relation to the cycle duration of the reference limb. Complementarily, we calculated the following spatial coordination variables: fore gap (FG; %) and hind gap (HG; %), corresponding to the distance between the footfalls of both limbs of a pair, fore and hind limb, respectively, relative to the stride length of the reference limb; and pair gap (PG; %), corresponding to the distance between the footfalls of the first limb of each pair to contact the ground as a percentage of the stride length of the reference limb (Abourachid, 2003; Abourachid et al., 2007; Maes et al., 2008). Positive PG values indicate that the hindfoot is placed on the support in front of the forefoot, while negative PG values correspond to the hindfoot being placed behind the forefoot. Finally, to assess regularity in limb coordination during locomotion, we compared PL values between successive sequences, thus defining the irregularity index (IrI) as the absolute value of the difference between PL of sequence n and PL of sequence $n - 1$ ($IrI_n = |PL_n - PL_{n-1}|$).

To test for differences in the mean values of both kinematic and coordination variables between overground and narrow-support locomotion, Mann–Whitney non-parametric tests were performed using SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA), since not all the data were normally distributed and homoscedasticity was not always observed. Values of $p < 0.05$ were considered statistically significant.

Regarding the relationship between each variable and speed, we used either the power equation or a linear model of regression, whichever was had a better r^2. All equations were calculated using least-squares regression (Sokal and Rohlf, 1995). Possible differences between the regression slopes of overground and narrow-support locomotion were accounted for using an F-test with a significance level of 0.05.

Table 1
Regressions on speed for overground and arboreal locomotion in cats and dogs. A power equation ($y = ax^b$) was used for all regressions except for L, in which a linear model of regression ($y = a + bx$) was used.

	Overground					Narrow support					
	a	b	CI_a	CI_b	R^2	a	b	CI_a	CI_b	R^2	p value
Cats											
F	1.898	0.628	1.859 to 1.937	0.598 to 0.658	0.799	1.930	0.646	1.853 to 2.009	0.602 to 0.689	0.677	>0.05
St	0.347	−0.720	0.340 to 0.356	−0.754 to −0.687	0.810	0.332	−0.813	0.326 to 0.355	−0.859 to −0.767	0.749	<0.01
Sw	0.183	−0.391	0.176 to 0.189	−0.445 to −0.337	0.325	*0.201*	*−0.071*	*0.190 to 0.213*	*−0.133 to −0.009*	*0.012*	–
L	0.258	0.296	0.244 to 0.272	0.270 to 0.322	0.548	0.246	0.322	0.229 to 0.262	0.284 to 0.360	0.409	>0.05
Dogs											
F	1.433	0.395	1.390 to 1.477	0.363 to 0.426	0.722	1.365	0.592	1.187 to 1.569	0.471 to 0.711	0.413	<0.01
St	0.509	−0.928	0.488 to 0.530	−0.970 to −0.884	0.887	0.608	−1.082	0.518 to 0.715	−1.221 to −0.943	0.639	<0.05
Sw	*0.250*	*0.061*	*0.237 to 0.262*	*0.009 to 0.112*	*0.023*	*0.216*	*−0.094*	*0.183 to 0.255*	*−0.236 to 0.048*	*0.013*	–
L	0.480	0.292	0.440 to 0.520	0.277 to 0.306	0.866	0.639	0.171	0.474 to 0.805	0.119 to 0.221	0.245	<0.01

Values in italics denote non-significant regressions.
CI_a, 95% confidence interval for a; CI_b, 95% confidence interval for b; F, cycle frequency (Hz); L, stride length (m); p value, significance of the comparison of slopes between overground and narrow-support locomotion ("–" denotes that no comparison could be made due to non-significant regressions); R^2, determination coefficient; St, stance phase duration (s); Sw, swing phase duration (s).

3. Results

A total of 425 APSs were obtained for cats in overground locomotion, while 403 sequences were filmed in the narrow-support situation. Cats did not show great difficulties in performing the exercise. On the contrary, they sometimes even performed a couple of locomotor sequences along the wooden bar, then turned around with no effort, and returned to the starting point. Speed values for cats ranged from 0.21 to 0.72 m/s. For dogs, only 134 APSs could be obtained for narrow-support locomotion, since they showed greater difficulties in performing the exercise. Even though they were used to agility training, they sometimes fell or jumped off the runway. Their speed ranged from 1.54 to 4.19 m/s. Since data from Maes et al. (2008) for overground locomotion comprised a much wider range of speeds (from 0.4 to 10.0 m/s), their dataset was reduced to 232 APSs that matched our speed range.

3.1. Cats

As expected, cats used significantly slower speeds in narrow-support than in overground locomotion (mean ± standard deviation: 0.42 ± 0.10 vs. 0.53 ± 0.11 m/s, respectively; $p < 0.001$). Regarding the slopes of either frequency or stride length, there were no significant differences between both situations (Table 1 and Fig. 2A,B). Nevertheless, the relative contribution of stance and swing phases differed in both situations. In narrow-support locomotion, stance phase duration decreased with increasing speed significantly faster than in overground locomotion (Table 1). Thus, although mean stance phase duration was longer in narrow-support locomotion at low speeds, these differences disappeared at higher speeds (Fig. 2C). Swing phase duration, while decreasing with speed in overground locomotion, was independent of speed in narrow-support locomotion (Table 1 and Fig. 2D) and also showed lower mean values (0.24 ± 0.04 vs. 0.22 ± 0.04 s, respectively; $p < 0.001$).

In both situations, cats used the lateral walk exclusively as their preferred gait. The values of temporal coordination variables (lags) were always close to the theoretical values defined by Abourachid (2003), although their variability slightly exceeded the classically accepted 5% (Hildebrand, 1966; Maes et al., 2008), especially for the hindlimbs (HL = $51.1 \pm 6.4\%$ and $49.3 \pm 6.9\%$ for overground and narrow-support locomotion, respectively; Table 2 and Fig. 3A,B). Temporal coordination between sequences was highly regular in both situations, since PL variation between consecutive APSs was on average <5% (IrI < 5%, Table 2). Pair lag values decreased from a mean of 83% to 75% as speed increased in both overground and narrow-support locomotion. Regarding significant differences in coordination variables between overground and narrow-support locomotion, FL values were significantly higher and HL and PL were significantly lower when cats moved along the wooden bar compared to overground locomotion. Finally, regarding spatial coordination, PG values were significantly lower in narrow-support locomotion (Table 2). In fact, when walking overground, cats usually placed each hindfoot in front of its corresponding forefoot (PG > 0%), while they placed the hindfeet behind the forefeet when moving along the wooden bar (PG < 0%). Together with some differences found in kinematic variables, this finding suggests the use of a different locomotor strategy in each situation.

Table 2
Comparison between coordination variables in overground and narrow-support locomotion in both cats and dogs. FG, fore gap (%); FL, fore lag (%); HG, hind gap (%); HL, hind lag (%); IrI, irregularity index (%); n, sample size; p value, significance of the comparison of mean values between overground and arboreal situations in cats (since the coordination patterns were unsteady in narrow-support locomotion compared to the steady gaits of the overground locomotion, significant differences in mean values for coordination variables could not be tested for in dogs); PG, pair gap (%); PL, pair lag (%); s.d., standard deviation.

	Cats					Dogs			
	Overground $n = 425$		Narrow support $n = 403$			Overground $n = 232$		Narrow support $n = 134$	
	Mean	s.d.	Mean	s.d.	p value	Mean	s.d.	Mean	s.d.
FL	49.5	3.3	50.9	4.0	<0.001	50.5	2.9	45.7	6.8
HL	51.1	6.4	49.3	6.9	<0.001	49.5	3.9	40.5	12.6
PL	80.2	5.1	79.5	4.2	<0.001	60.8	18.2	60.7	9.3
FG	50.3	4.1	50.5	5.1	0.875	50.1	2.9	45.5	6.7
HG	50.7	5.1	50.3	5.9	0.265	50.3	4.0	40.6	11.7
PG	6.8	7.3	−5.7	9.0	<0.001	11.1	17.8	5.7	11.0
IrI	3.5	2.8	2.6	2.2	0.091	3.3	3.2	6.6	4.6
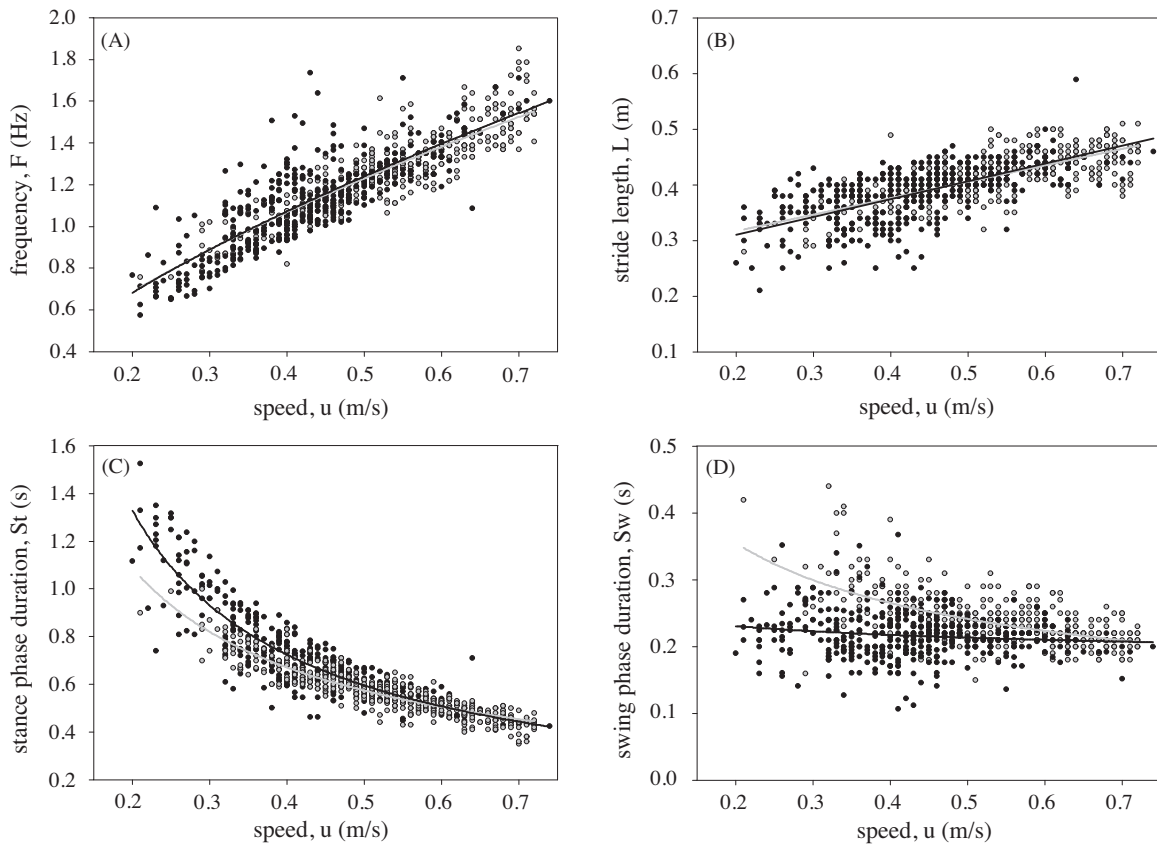
Fig. 2. Relationship between speed and (A) cycle frequency, (B) stride length, (C) stance phase duration, and (D) swing phase duration in cats. Grey dots represent overground locomotion data, black dots represent data from narrow-support locomotion.
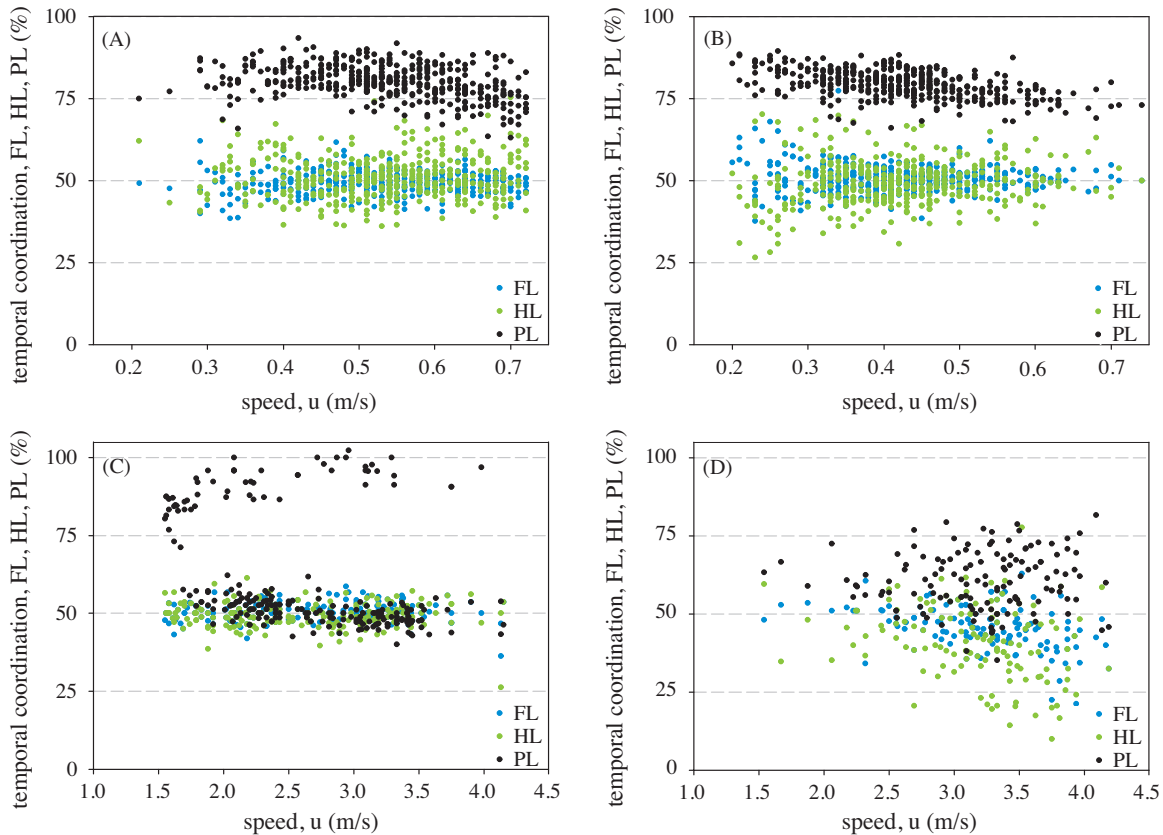
Fig. 3. Temporal coordination in (A and B) cats and (C and D) dogs. Graphs on the left correspond to overground locomotion (A and C), while those on the right represent narrow-support locomotion (B and D). Blue dots represent fore lag (FL), green dots represent hind lag (HL), and black dots represent pair lag (PL).
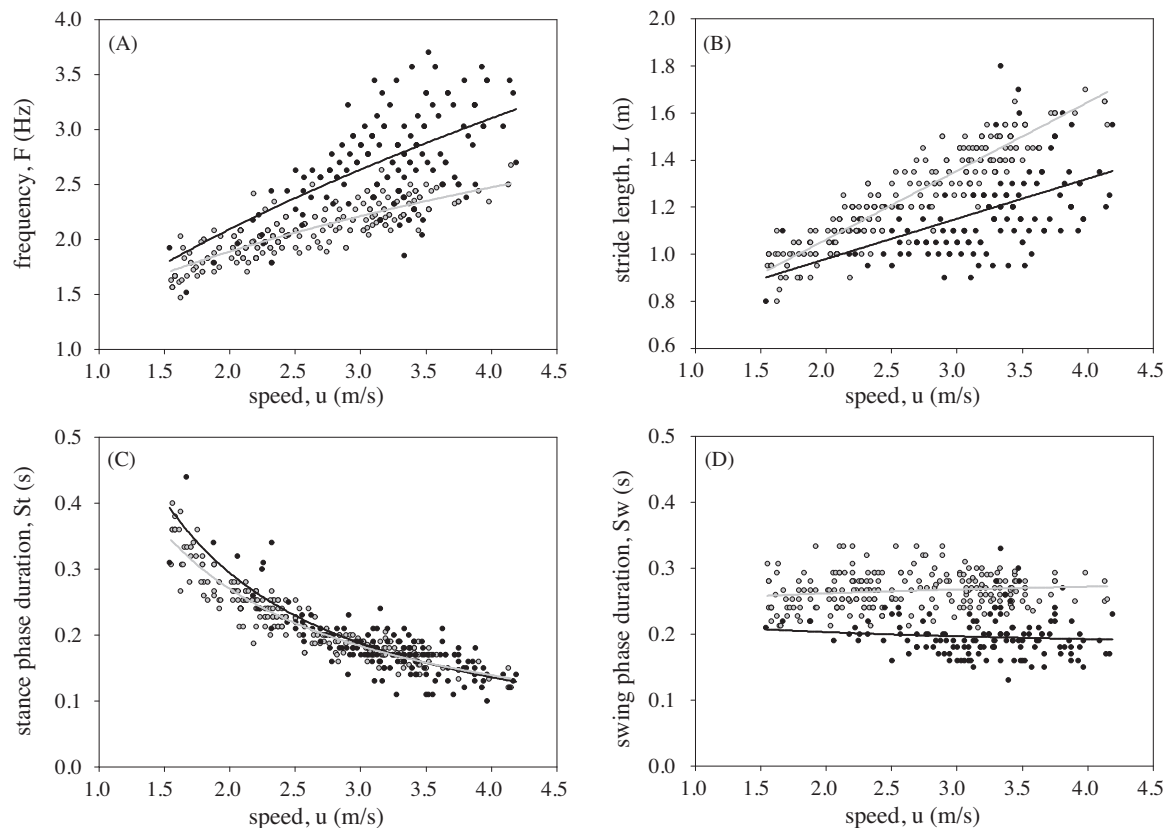
Fig. 4. Relationship between speed and (A) cycle frequency, (B) stride length, (C) stance phase duration, and (D) and swing phase duration in dogs. Grey dots represent overground locomotion data, black dots represent data from narrow-support locomotion.

3.2. Dogs

Dogs tended to perform the exercise at high speeds: the mean speed for narrow-support locomotion was 3.20 ± 0.52 m/s, a value close to the top speeds found for symmetrical gaits in the study of Maes et al. (2008). Regarding the rest of the kinematic variables, cycle frequency increased significantly faster in narrow-support locomotion, with the slope obtained for the 'arboreal' situation almost 1.5 times the slope obtained for overground locomotion (Table 1 and Fig. 4A), which suggests the use of different loco-motor strategies in each situation. On the other hand, the slope of stride length was significantly lower in narrow-support locomotion (Table 1 and Fig. 4B), probably relating to a consistent reduction or even lack of whole-body aerial phases in narrow-support locomotion. Only 24.6% of narrow-support APSs included a whole-body aerial phase, whose duration was on average only $4.7 \pm 3.1\%$ of cycle duration. Stance phase duration decreased significantly faster in narrow-support locomotion (Table 1 and Fig. 4C). Swing phase duration was independent of speed in both situations (Table 1 and Fig. 4D), and, as observed in cats, it was significantly shorter when dogs moved on the catwalk (0.27 ± 0.03 vs. 0.20 ± 0.03 s for over-ground and narrow-support locomotion, respectively; $p < 0.001$).

Even though we considered the same range of speeds, the coor-dination patterns employed in overground and narrow-support locomotion were different. When moving overground, dogs used almost exclusively symmetrical gaits (FL = HL = $50 \pm 5\%$), with the trot as their preferred gait: of the 232 APSs analysed for over-ground locomotion, 30 (12.9%) corresponded to lateral walk, 30 (12.9%) to pace, 1 (0.4%) to transverse gallop, and 171 (73.7%) to trot. On the other hand, dogs preferred asymmetrical coordination patterns (FL $\neq 50 \pm 5\%$ and/or HL $\neq 50 \pm 5\%$) in narrow-support locomotion, since only 28 out of 134 APSs (20.9%) were strictly sym-metrical. Temporal coordination between sequences in overground locomotion was highly regular (IrI = $3.3 \pm 3.2\%$; Table 2), contrary to what was found in narrow-support locomotion, since IrI exceeded on average the 5% threshold (IrI = $6.6 \pm 4.6\%$; Table 2). Given that these high IrI values, together with the high standard deviation of coordination variables in narrow-support locomotion (6.8 and 12.6 for FL and HL, respectively; Table 2), make the link to gaits difficult to express, we prefer to speak of a "coordination pattern" instead of a "gait". Only about 92 of the 134 'arboreal' sequences (68.7%) appeared like gaits classically defined in locomotion stud-ies: we found 12 (9.0%) sequences of gallop-like coordination, 45 (33.6%) corresponding to canter-like coordination, and 35 (26.1%) to trot-like coordination. Since the coordination patterns in the narrow-support situation were unsteady compared to the steady gaits of the overground situation, significant differences in mean values for coordination variables could not be tested for in dogs (Table 2 and Fig. 3C,D).

4. Discussion

4.1. A common strategy for non-arboreal specialists

The main strategy for cats to adapt to the arboreal situation was to use slower speeds (with the corresponding adjustment of all speed-related variables, e.g., longer stance phase duration), which is generally associated with lower peak vertical forces (Demes et al., 1994; Schmitt and Lemelin, 2002). Similar results were obtained by Lammers and Biknevicius (2004) when studying the dynamics of arboreal locomotion in the grey short-tailed opossum (*Monodelphis domestica*), a smaller non-arboreal specialist with limited grasping abilities that nevertheless navigates frequently on arboreal sub-strates. Furthermore, these authors also reported an increase in
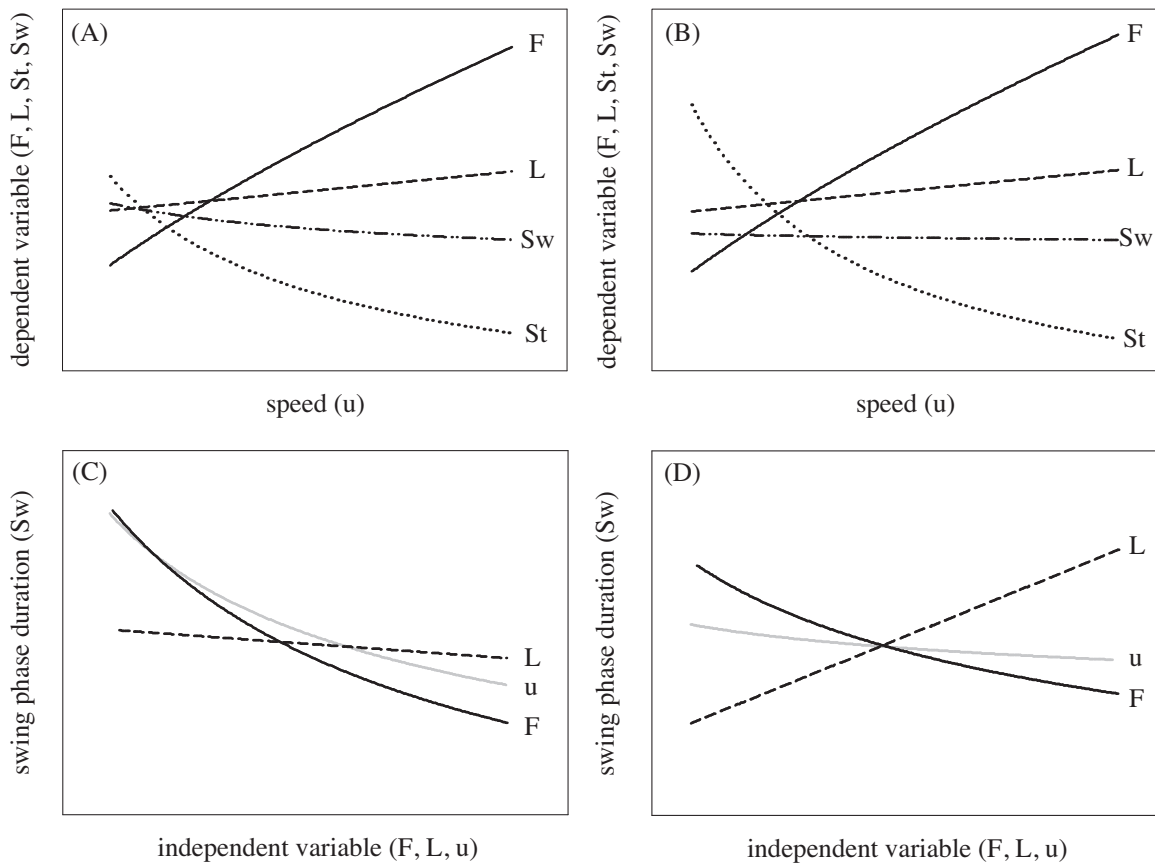
Fig. 5. Relationships (A and B) between speed and several kinematic variables, and (C and D) between swing phase duration and cycle frequency, stride length, and speed in cats. Plots on the left (A and C) represent overground locomotion data, while those on the right (B and D) correspond to narrow-support locomotion. *Abbreviations*: *F*, cycle frequency (Hz); *L*, stride length (m); St, stance phase duration (s); Sw, swing phase duration (s); *u*, speed (m/s).

duty factor in an arboreal situation, and significantly steeper slopes when comparing stance phase duration vs. speed in the arboreal trials with those obtained for overground trials, as observed in the present study (Table 1 and Fig. 2C). Thus, in accordance with our prediction, it seems that there is a common strategy for small and medium-sized non-arboreal specialists to increase their stability when in an arboreal situation.

Swing phase duration was the only variable that was modified during the cats' narrow-support locomotion in a way not predicted by speed: it decreased significantly with speed when cats moved overground, but its variation was independent of speed in narrow-support locomotion (Fig. 5A and B). Given that speed is directly related to changes in cycle frequency (F) and/or stride length (L), we studied the relationship between these variables and swing phase duration (Sw; Fig. 5C and D). Cycle frequency is inversely related to swing phase duration ($F = [St + Sw]^{-1}$), while in each cycle stride length is determined during the swing phase. Therefore, Sw should decrease with increasing F, and it should also be related to L in some way. As expected, as cycle frequency increased, swing phase duration decreased in both the arboreal and flat ground situations (Fig. 5C and D). Swing phase duration and stride length were not significantly related in overground locomotion in cats (Sw $= 0.280 - 0.099L$; $R^2 = 0.014$; Fig. 5C), suggesting the existence of factors other than swing phase duration to explain the increase in stride length with speed in this situation (e.g., greater angular velocities of the limb during the swing phase). On the other hand, longer strides were directly related to an increase in swing phase duration in narrow-support locomotion (Sw $= 0.114 + 0.270L$; $R^2 = 0.163$; Fig. 5D). During film analysis, it was frequently observed

that, when cats got out of balance, they quickly leaned their feet on the bar, shortening considerably swing phase duration and thus reducing stride length. It was also observed that, when there were no balance issues, cats usually made tentative steps before definitely placing their forefeet on the bar, allowing them a steadier grip, but in turn increasing swing phase duration. These observations support the relationship between swing phase duration and stride length, but they also suggest that variations in swing phase duration would be more related to balance than to speed. In summary, during undisturbed overground locomotion in the cat, the relationship between swing phase duration and speed mirrors the relationship between cycle frequency and speed (Fig. 5C). During 'arboreal' locomotion, however, a significant relationship appears between swing phase duration and stride length, probably related to the search for stability. Thus, there is a direct relationship between Sw and L, and an inverse relationship between Sw and F. This conflicting compromise between increasing speed and maintaining balance probably renders non-significant the relationship between swing phase duration and speed (since $u = LF$) (Fig. 5D).

A possible explanation for the lower pair gap values found in narrow-support locomotion could be the crouched posture adopted by most cats and several dogs when moving along the elevated support, which is characteristic of mammals moving on narrow supports (Cartmill, 1985; Schmitt and Lemelin, 2002; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). The use of a crouched posture increases stability by bringing the centre of mass closer to the support, but it also hampers limb protraction, thus causing the hindlimbs to touch the ground not as far ahead as typically observed, and reducing pair gap values. As suggested by

Lepicard et al. (2006), for mice in potentially dangerous environmental conditions, the reduction of swing phase duration and the use of a crouched posture are a function of the animals' risk assessment of the environment.

Finally, during film analysis, it was observed that cats placed their feet obliquely to the support. That is, during locomotion on narrow supports the lower arm was kept in an adducted position during the stance phase. These observations agree with previous results on primate arboreal locomotion (Schmitt, 2003a). When comparing mediolaterally applied forces and joint angles during terrestrial and arboreal locomotion in primates, Schmitt (2003a) found that most of the studied animals showed a higher degree of adduction on the arboreal support. Lower arm adduction in the cat is probably accomplished thanks to the angle of the olecranon fossa relative to the long axis of the humerus, which has been previously related to living in densely structured habitats (Gonyea, 1978). In the case of domestic cats, this angle is about 9°, at an intermediate position between the cheetah, *Acinonyx jubatus* (3°; highly cursorial, open terrain dweller), and the arboreal margay cat, *Leopardus wiedii* (13°). The oblique placement of the feet creates a larger support polygon, since the feet are no longer collinear, thus increasing stability. Furthermore, it probably reorients ground support forces inwards to the support, which prevents slipping off it and reduces lateral oscillations of the centre of mass (Schmitt, 2003a; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). This finding further validates the use of a narrow, square bar to simulate arboreal supports.

4.2. Dynamic stability over balance in completely terrestrial species

As shown above, dogs tended to perform the 'arboreal' exercise at high speeds, probably relying on dynamic stability rather than on balance. To increase their speed, dogs reduced cycle duration significantly by shortening the swing phase, which recalls the strategy used by cats when out of balance. This behaviour thus seems characteristic of locomotion on narrow supports in both cats and dogs. It has been demonstrated that increased angular velocities during limb retraction in the swing phase prior to touch-down are a simple strategy to increase the stability of spring-mass running (Seyfarth et al., 2003). These increased angular velocities could account for the observed reduction of swing phase duration during 'arboreal' locomotion in dogs.

The strategy of dogs during 'arboreal' locomotion involved other striking features, namely the reduction, or even loss, of whole-body aerial phases, and important changes in coordination. Thus, it seems that completely terrestrial mammals (dogs) use a different strategy to gain stability on narrow supports from non-arboreal specialists. Considering the overlapping speed range (1.54–4.19 m/s), 72.3% of the sequences performed overground included a whole-body aerial phase (83.1% when excluding lateral walk), while only 26.3% included an aerial phase on the narrow support. The reduction of whole-body aerial phases probably was a strategy to achieve lower peak vertical forces, which reduces vertical oscillation of the centre of mass and of the support, increasing stability. This strategy has also been reported for overground locomotion in elephants (Hutchinson et al., 2006), and for arboreal ambling and cantering in primates, for which it has also been described as a strategy to maintain a secure grip on the branch, thus increasing the importance of this strategy in arboreal locomotion (Schmitt, 1999; Schmitt et al., 2006).

Regarding coordination, while dogs favoured symmetrical gaits, especially the trot, when moving overground at the specific speed range considered in this study (1.54–4.19 m/s), they used mainly asymmetrical coordination patterns when moving along the elevated narrow support. Although 48% of the APSs of narrow-support
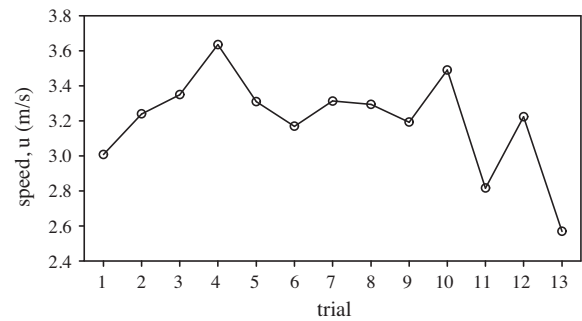

Fig. 6. Mean speed values of dogs for each successive trial of narrow-support locomotion.

locomotion could not be classified into any classically defined gait, 34% could be attributed to canter-like coordination, and 9% each to transverse gallop-like and trot-like coordination. In canter, only one of the synchronised limb couplets characterising the trot is retained, thus, by using canter-like coordination, dogs gain an additional functional step per sequence, which grants them another chance to modify their kinematics and coordination (in contrast to just two functional steps in trot; Lee et al., 1999). Furthermore, coupled with whole-body aerial phase reduction, canter-like coordination allows dogs to lean on three feet during part of the cycle, thus reducing bipedality (only two feet on the ground at the same time), which in turn enhances stability when moving forward (Hildebrand, 1980; Cartmill et al., 2002). Both canter-like and trot-like coordination are characterised by periods of diagonal bipedality, which provides mechanical stability during running, given that touch-down synchronisation of diagonal limbs opposes the forces that tend to rotate the body in both its transverse (pitch) and sagittal (roll) axis (Hildebrand, 1985; Lee et al., 1999; Cartmill et al., 2002). This may also explain why a pace-like coordination, less stable since it maximises unilateral bipedality (Cartmill et al., 2002), was never observed in narrow-support locomotion, while dogs used the pace overground (Maes et al., 2008).

These results agree with the work of Schmitt et al. (2006) in primates, whose preferred gait in asymmetrical running was the canter when moving either along a horizontal pole or overground. In the same study, Schmitt et al. (2006) stated that both ambling gaits and canter allow animals to maintain at least one foot in contact with the support during the stride, that is, to eliminate whole-body aerial phases. This loss of whole-body aerial phases cannot be accomplished at high speed trotting (e.g., in our data for dogs in narrow-support locomotion, 45.7% of the trot-like sequences included a whole-body aerial phase, whereas only 11.1% of the canter-like sequences did). They also noted that both canter and ambling gaits account for reduced periods of bipedality. According to these authors, these properties of ambling gaits and canter increase the animal's stability by lowering peak vertical forces, thus reducing vertical displacement of the centre of mass and vertical oscillation of the support. It would be interesting to study substrate reaction force patterns in cats and dogs, as has been done in primates and opossums (Schmitt, 1999; Schmitt and Lemelin, 2002; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010), to assess this decrease in peak vertical forces when these animals advance in an arboreal situation.

Finally, it could be argued that the preference of dogs for high speeds in narrow-support locomotion could be a consequence of their agility training. Although it probably influenced their first trials traversing the elevated runway, since the highest observed speed values correspond to the first trials, there might have been a learning process during the subsequent trials, in which the dogs progressively decreased their speed on the runway (Fig. 6). Never-

theless, due to the low sample size (only 3 dogs performed more than 10 trials), no significant correlation could be found between speed and trial number ($p = 0.399$).

4.3. Conclusions

Our study of the kinematics and coordination in the cat points to the existence of a global strategy for medium-sized (cats) and small (opossums) non-arboreal specialists when moving on narrow, elevated supports. This strategy consists of the use of low speeds, probably to reduce peak vertical forces, hence to reduce the oscillations of the centre of mass and those of the support. No change in gaits is needed to maintain balance.

In contrast, the completely terrestrial dogs showed greater difficulties to adapt to narrow-support locomotion. They moved at high speeds to gain in dynamic stability, using unsteady asymmetrical coordination patterns, suggesting constant readjustments in limb coordination. The reduction of whole-body aerial phases limited vertical oscillation of the centre of mass.

The only universal strategy observed was the maximisation of contact time between the animal and the support by reducing swing phase duration and also by the use of a crouched posture, which probably reduces oscillation of the centre of mass.

Acknowledgements

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