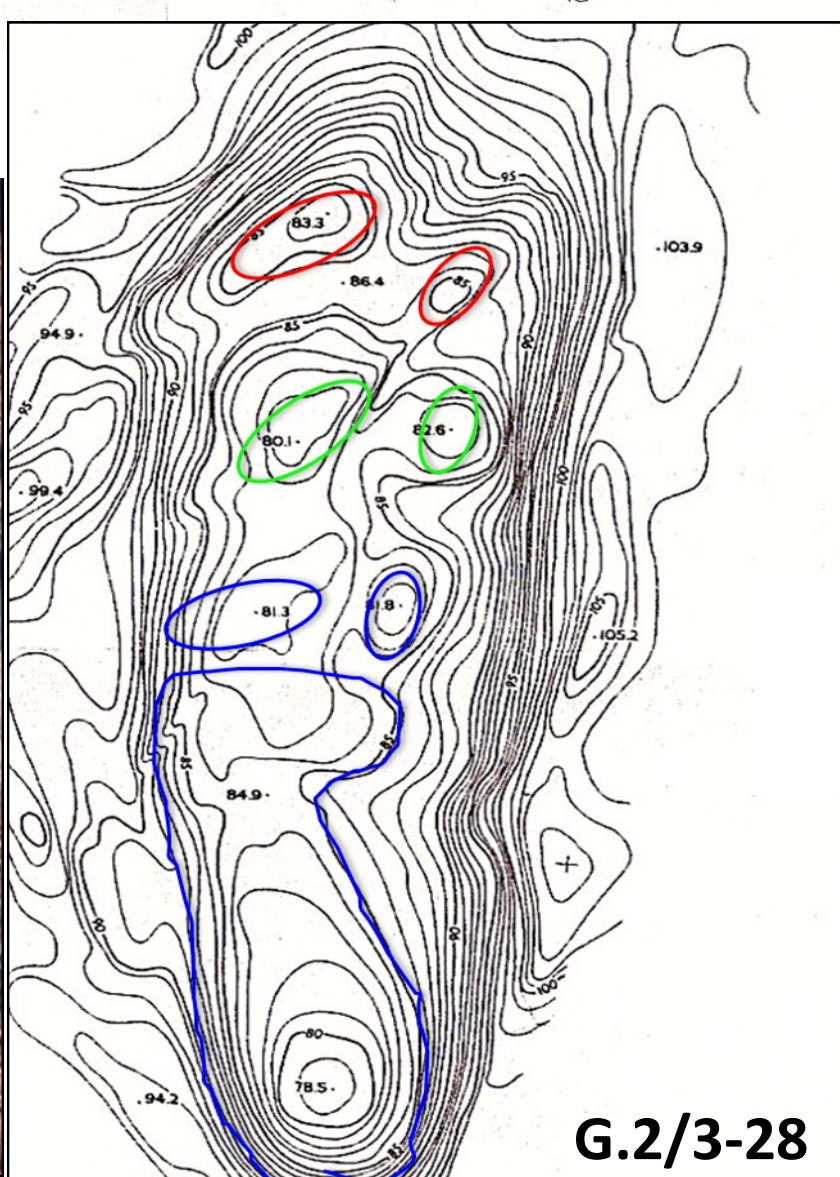


Group Locomotion in the Laetoli Trackway: An Intriguing Case of Direct Register

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Introduction



The ancient set of hominin tracks discovered at Laetoli in Tanzania, Africa, by Mary Leakey and her associates in 1978 is an approximately 24-meter trackway thought to be evidence left from a species of *Australopithecus* traversing the landscape (Figure 1). Footsteps from what was originally understood to be three individuals (G.1, G.2, and G.3) are represented in the trackway (Figure 2). The interpretation of the footsteps suggested that G.1 walked alone on the west side of the trackway, while G.3 followed G.2, stepping directly into G.2's footsteps on the east side of the trackway. This behavior of walking in another individual's footsteps, defined as direct register, is unusual. Anatomically modern humans (AMH) are known to walk in direct register under certain circumstances, such as when it supports travel efficiency, group security, or for ritual purposes (Boyd 2012). Adding to the intrigue of the Laetoli trackway, later analysis revealed that the number of individuals present was four, not three, and that three of the individuals exhibited 100-percent direct register walking (Boyd 2012). This new evidence for an increased number of individuals represented in the trackway is important, as it suggests intentional use of direct register walking by a group of individuals. Furthermore, the individuals represented in the trackway display a range of different statures (Leakey and Harris 1987), which would normally create different strides in their gait (Martin 2011). Conclusions presented by Boyd (2012) suggested a need to examine direct register walking in other species in order to provide insight into the origin of the behavior. Evidence of direct register walking can easily be found when examining other species (Table 1). Like AMH, many mammals direct register walk for travel efficiency when in certain terrain. For example, deep snow was found to cause ursids (bears) and snow macaques to use direct register to support travel efficiency (Figure 3). This raised the question of whether walking on wet volcanic ash might require use of direct register for the Australopithecus. Using the Leakey and Harris (1987) map of a 5-meter section of the trackway as a standard of direct register (Figure 4), with consideration for differences in perspective between each case, the research presented here tests the presence of direct register behavior in AMH and chimpanzees to determine if direct register walking occurs in these species. In addition to documenting the presence or absence of this behavior, this research examines the conditions (i.e., terrain, social dynamics, environmental conditions, etc.) that may give rise to direct register movement.

Direct Register Mapping Methods

Direct register walking is defined as an individual walking in another individual's footsteps. To measure direct register walking in the AMH and chimpanzee study cases presented here, mapping of individual foot placement was required. However, these trackways would be viewed from the side, whereas the Laetoli trackway was viewed from above (Figure 4). In addition, all of the trackways were not made from a normal angle to the camera. The methods listed below were conducted for mapping foot placement of both species, accounting for the difference in perspective:

1. A screen capture was recorded for each individual's footprint and then pasted into Powerpoint (Figure 5).
2. Color-coded markers were overlaid onto every right and left foot placement for each individual.
3. Each individual of the group was color-coded to keep track of independent movement.
4. Once all footprint mapping was complete, all individuals' trackways within a group were assessed to determine if direct register occurred between individuals.
5. Updated overlap criteria were: ≥ 50 percent longitudinal overlap, and ≥ 75 percent lateral overlap along the axis of travel.

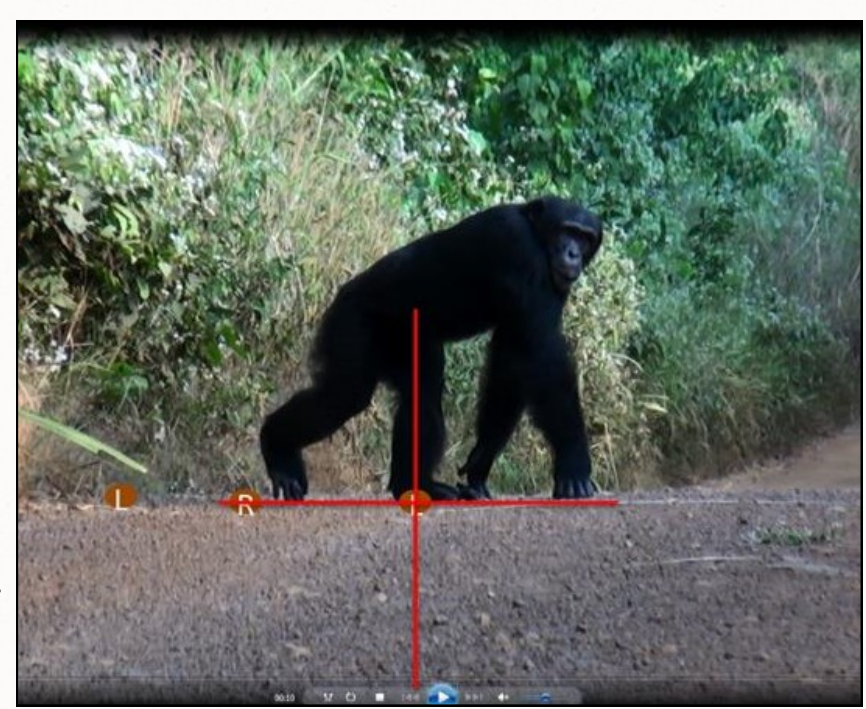
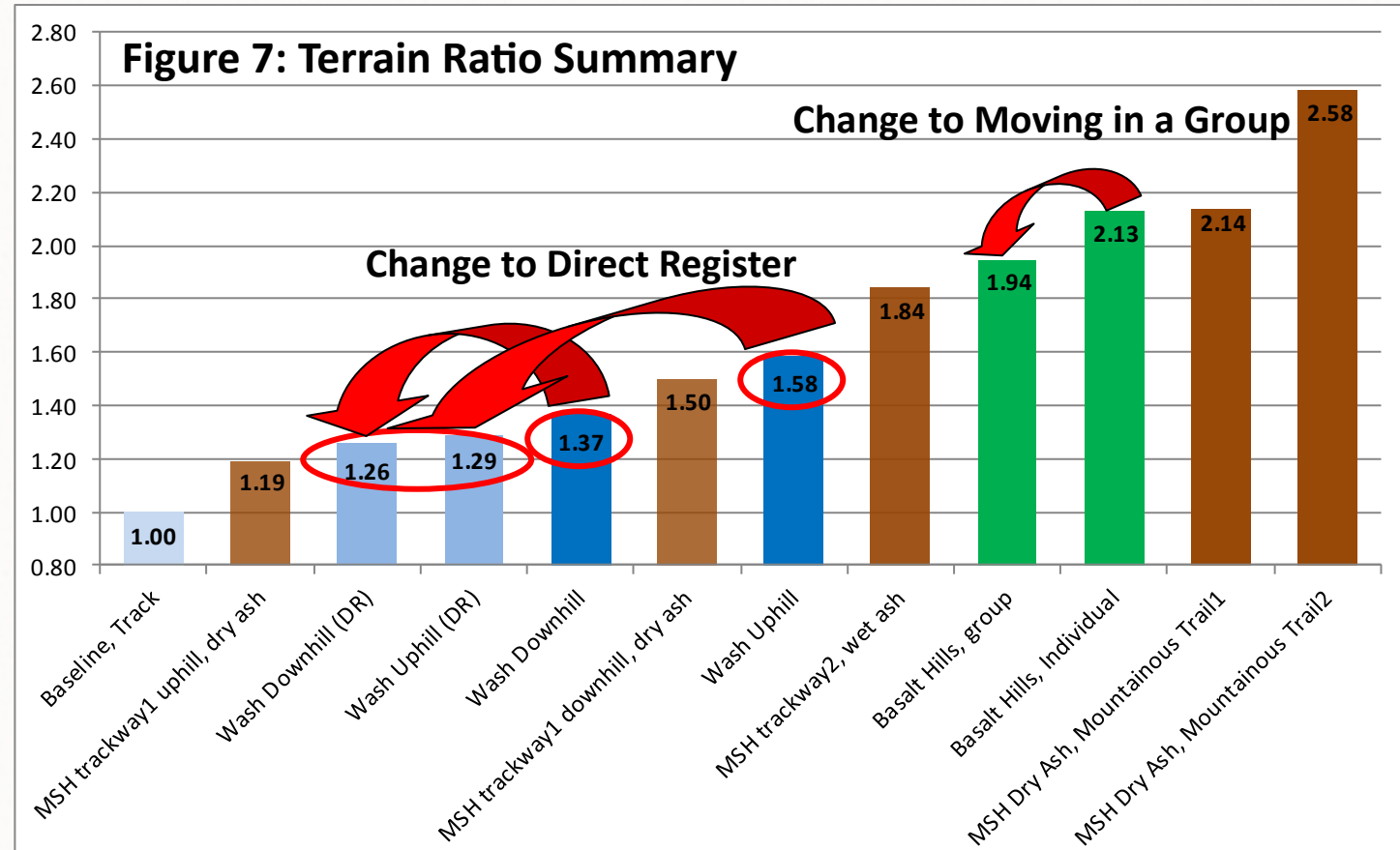


Figure 5: Footstep Mapping of Chimpanzee

AMH Studies

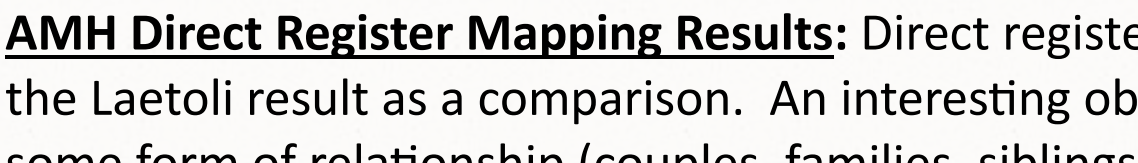
Sample Population: To determine if AMH engage in direct register walking and under what conditions they might, speed and terrain were examined as potential factors influencing direct register (Figure 6). These were then compared to baselines to determine if they were significant. The different sample populations examined are as follows:

1. Subjects from Pima Community College in Tucson, AZ, provided data for the influence of terrain difficulty on walking speed, and on direct register walking.
 - a. Terrain difficulty is defined as a ratio of baseline speed (1.0) divided by selected terrain speed.
 - b. The terrain types examined here included: A flat, maintained track to establish baseline speeds, a sand/gravel wash in the Sonoran Desert, uneven basaltic highlands in western AZ, and on and off-trail volcanic ash at Mt. St. Helens.
2. Hiking groups climbing Mt. St. Helens were observed to gather frequency data for direct register walking (Figure 8).
3. Video analysis of the Boston bombing suspects was used to gather direct register/familial relationship data (Figure 9).



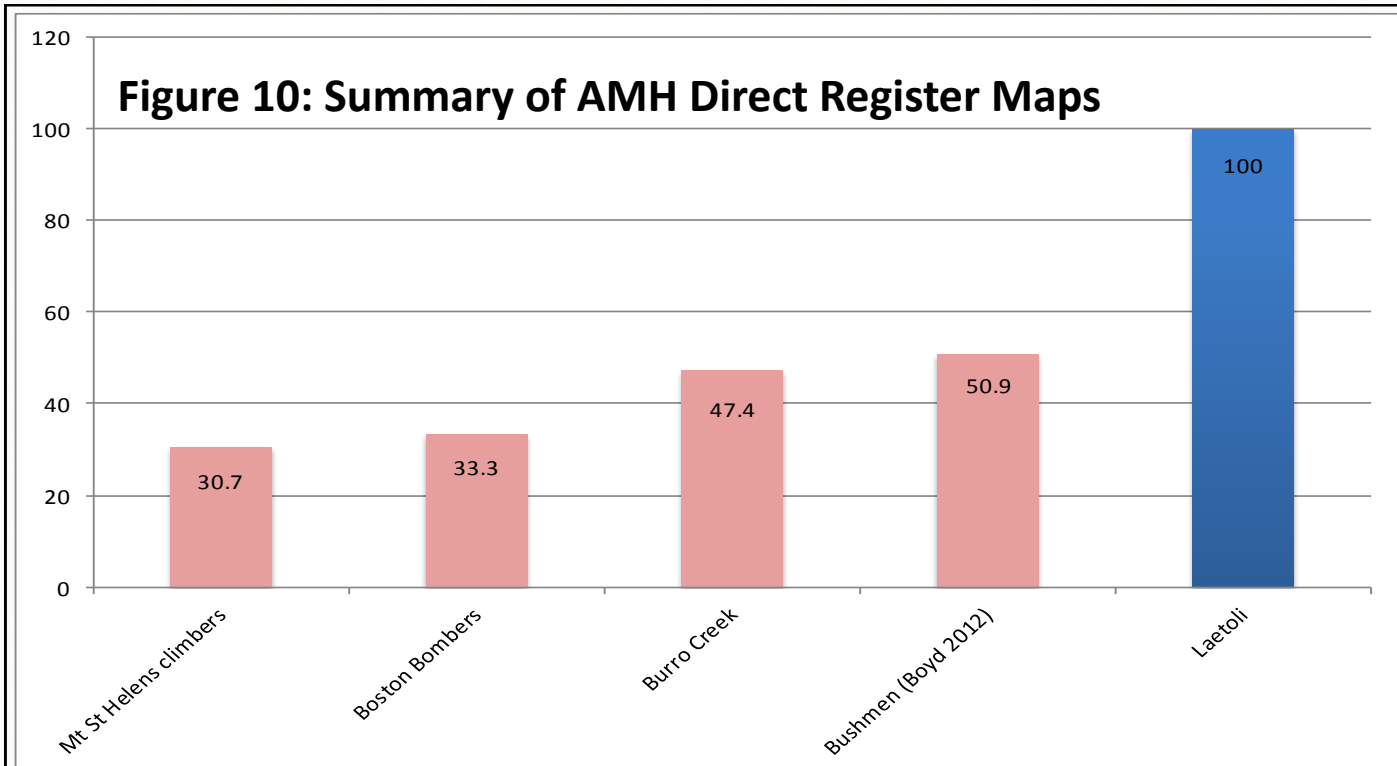
Terrain Difficulty Results: The overall effect of walking on volcanic ash, like the Laetoli hominins did, did not cause the AMH subjects to resort to a high degree of direct register walking. However, when the sand/gravel wash subjects intentionally walked in direct register, terrain difficulty ratio decreased by an average of 0.20. One subject in basaltic highlands showed a terrain difficulty ratio decrease of 0.19 when walking in a group versus walking alone. These results suggest walking in a group, or walking in direct register increases efficiency for AMH traveling across a landscape. Figure 7 summarizes all of the terrain ratio studies.

Figure 6: AMH Study Terrain Types



AMH Direct Register Mapping Results: Direct register mapping results are shown in Figure 10, and includes the Laetoli result as a comparison. An interesting observation during these studies was that individuals in some form of relationship (couples, families, siblings), as well as groups with a large number of same sex individuals, tended to show higher degrees of direct register. This raised a question whether individuals in relationships, or those of the same sex, might produce higher degrees of direct register. This question arose at the same time of the Boston bombing, and the suspect video released by the FBI indicated the two suspects might be walking in direct register. Analysis of the video showed 33.3 percent of the tracks studied were in direct register. These siblings of different stature maintained similar stride length as they moved at the same speed, despite their different statures.

Conclusions for AMH Studies: The AMH studies did not suggest that difficult terrain, such as volcanic ash, would cause groups of humans to walk in direct register. However, several other factors came to light regarding the use of direct register walking. First, terrain ratio data indicated that walking in direct register may be a more efficient form of group locomotion, even in less difficult terrain, such as sand/gravel. In addition, walking in a group versus alone may also provide an increase in travel efficiency. Second, after mapping different groups of AMH for direct register, a question arose about the effect of relationship between individuals on the degree of direct register a group might exhibit. One couple at Mt. St. Helens produced a direct register map of 66.6 percent, and had the Boston bomber siblings walked the same line, they would have produced a percentage of over 83 percent direct register. Also, data from this study suggests sex composition of a group impacts the frequency of direct register occurrence. Three MSH groups (assumed to be friends) consisted of two all-male groups and one heavily populated with females (7 female, 2 male). Each group walked in direct register percentages over 46 percent of the mapped time. These questions about relationship and direct register were added to the chimpanzee study.



Conclusions The terrain study did not find for volcanic ash to be a factor in causing AMH to walk in direct register. However, intentional use of direct register walking, and walking with a group showed improvements in travel efficiency when walking on the same substrate. In addition, the Mt. St. Helens studies and analysis of the Boston bombing suspects raised questions about how relationship and sexual composition within a group might affect direct register walking. The chimpanzee study showed moderately high levels of direct register walking, greater than or equal to 30 percent, appeared to occur as a result of close proximity, with a secondary influence by stature difference. Factors within the group affected proximity, such as relation to the alpha male, mothers and daughters staying together, and females forming cohorts to the exclusion of others within the group. It also does not appear that the chimpanzees engaged in direct register walking intentionally. This highlights the importance of the behavior exhibited by the Laetoli group, where a 100-percent occurrence of direct register walking was exhibited by at least three individuals of different stature. Why *Australopithecus* found it advantageous to engage in such a behavior is still unknown, but the research presented here does provide some insight. Three individuals walking in direct register is not a coincidence. Further, the factors of physical and temporal proximity seen with chimpanzees continues to strengthen the argument that the Laetoli individuals moved as a group, and that volcanic ash was probably not a driving force influencing direct register walking. There may be other factors, such as long distance travel, driving this behavior. This raises a question of how much cognition is required to exhibit such a behavior. Walking in direct register does require a form of "track awareness," which humans are known to have. Considering this, it could be inferred that *Australopithecus afarensis* had track awareness as well. An important point, however, is that chimpanzees and *Australopithecus afarensis* have similar cranial capacities (Leiberman 2011), which infers similar cognitive capability. This study brings into question the cognitive organization of *Australopithecus afarensis*.

Table 1: Direct Register Species Examination

Species	Direct Register?	Percent	Reason	Source
Ursid (Bears)				
Polar Bear	Yes	100	Terrain (snow)	Planet Earth video
Brown Bear	Yes	100	Terrain (tundra)	Waythomas 2012
Primates				
Macaque	Yes	100	Terrain (snow)	Youtube video
Human	Yes	30-100	Terrain, Security Ritual	Boyd 2012
Chimpanzee	Unk	TBD		-
Gorilla	Unk	-	Not tested	-

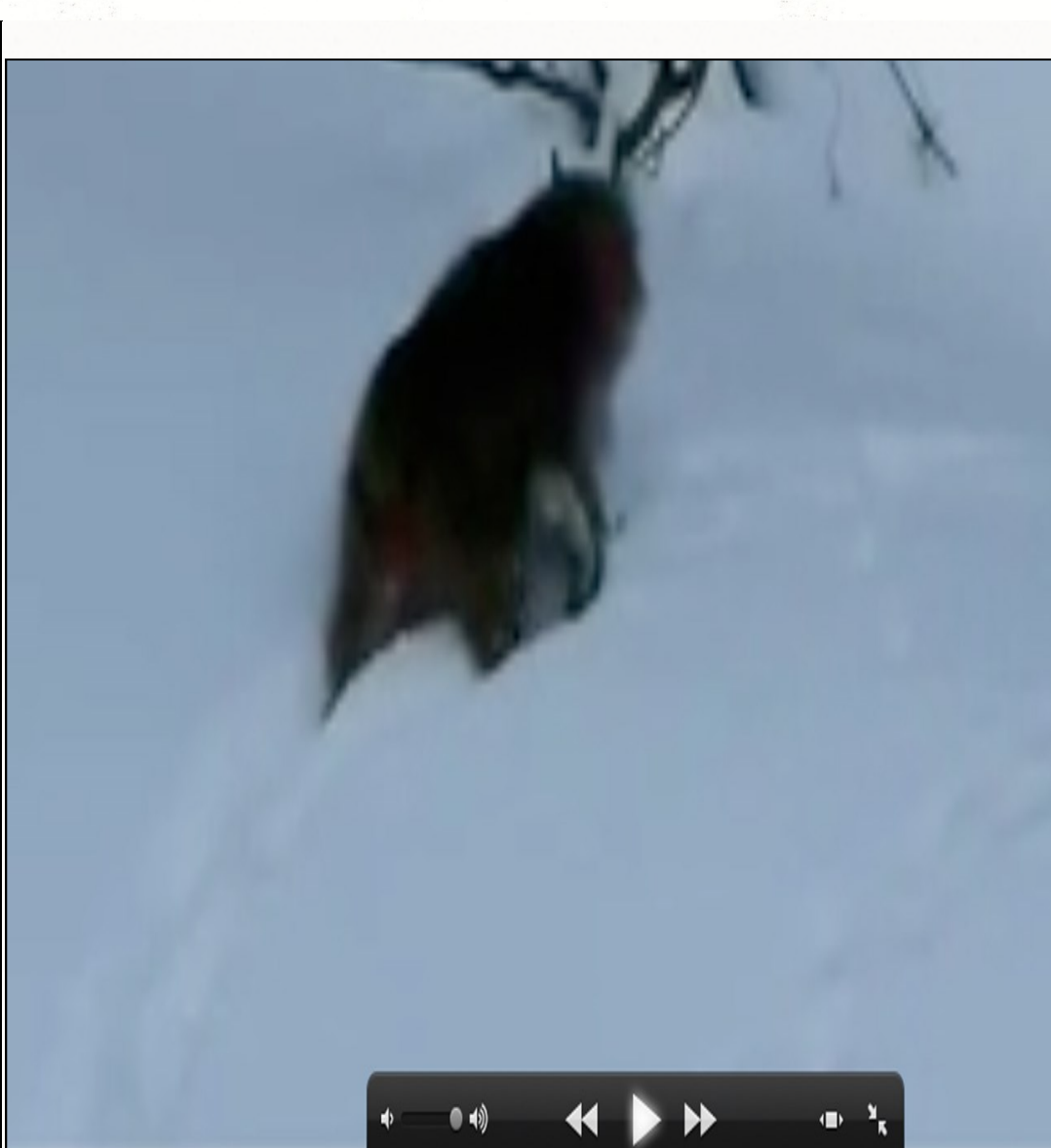


Figure 3: Snow Macaque in Deep Snow. http://www.youtube.com/watch?v=RFD7nn_hLg

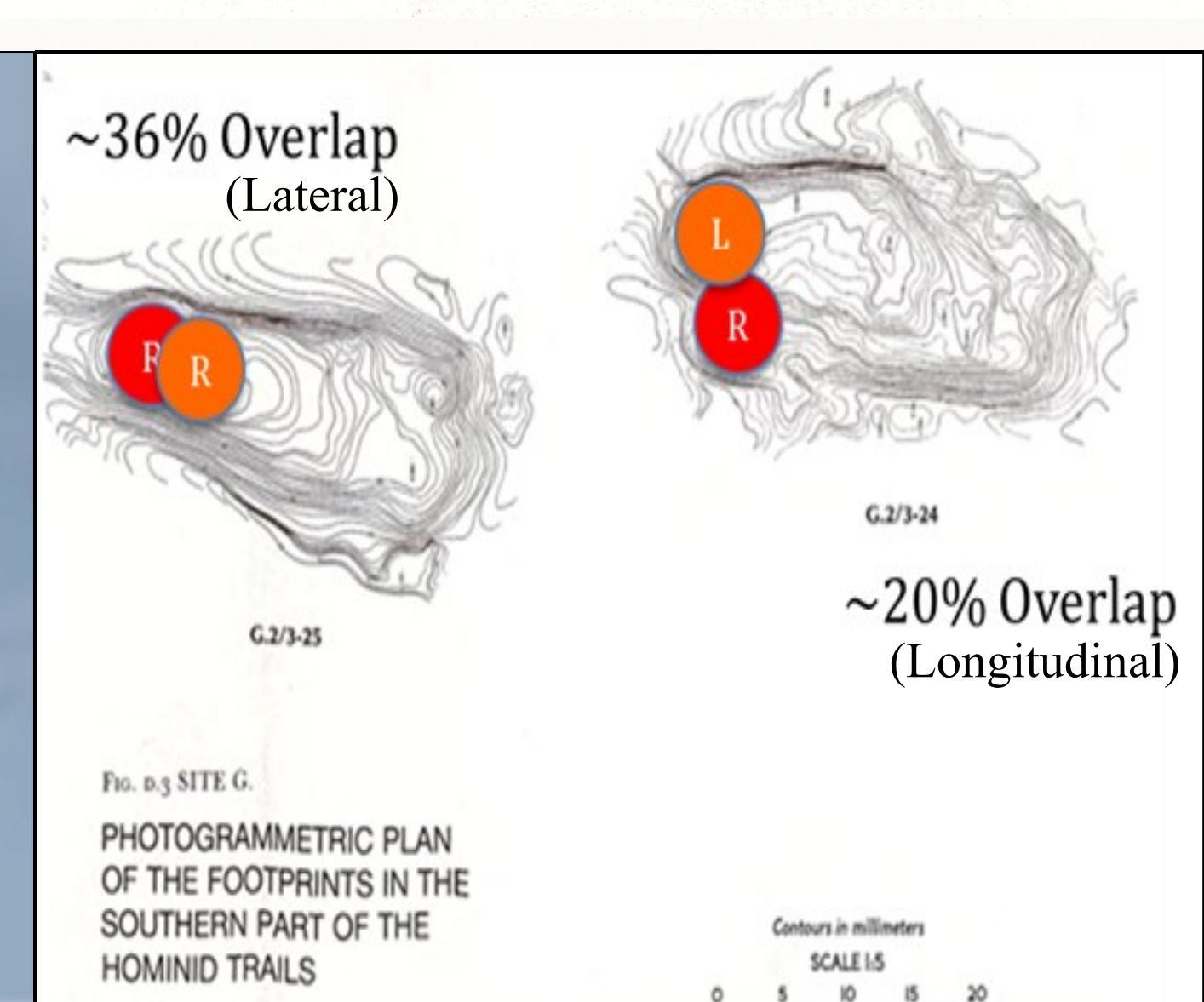


Figure 4: Maximum Lateral and Longitudinal Track Misalignment in Laetoli Trackway Used to Define Direct Register (Boyd 2015, Leakey and Harris 1987)

Chimpanzee Study

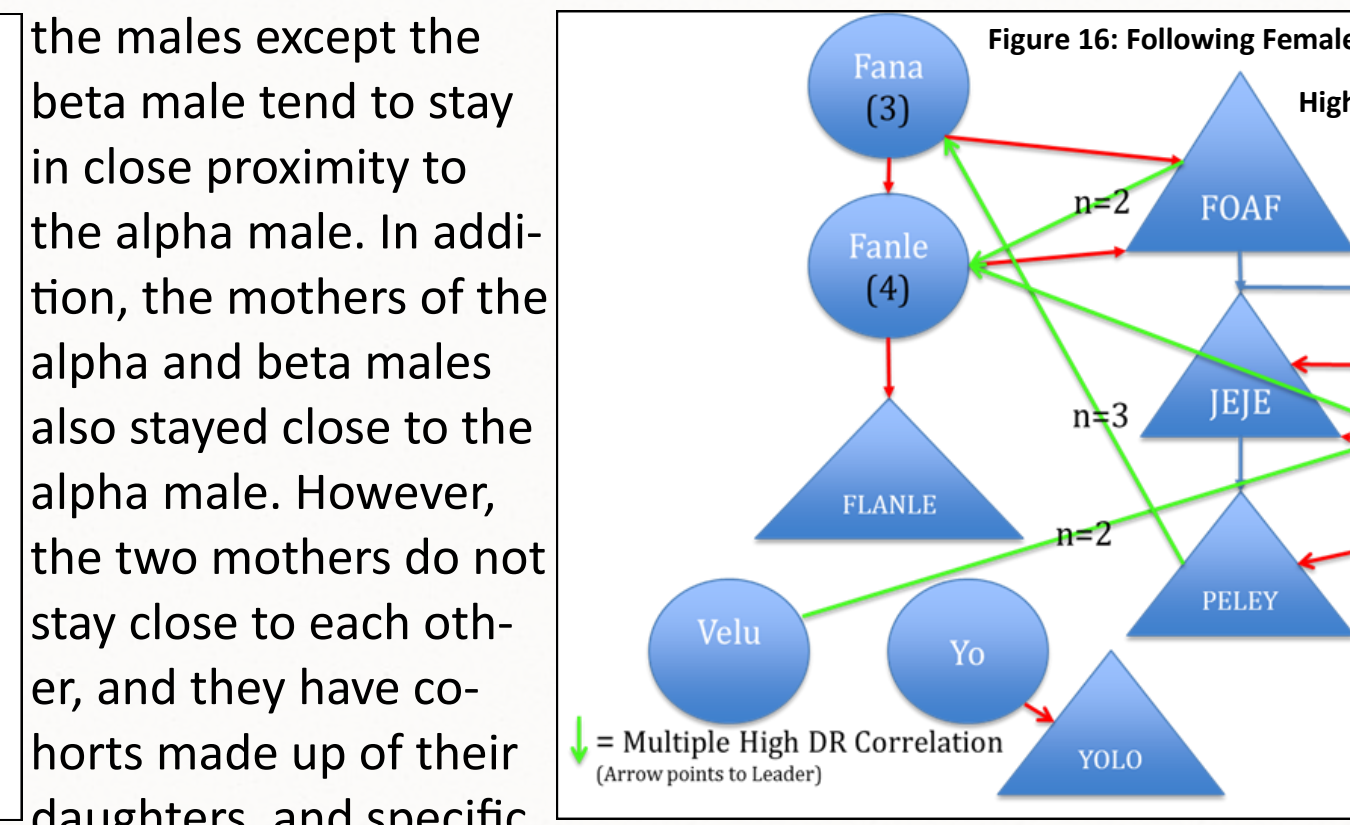
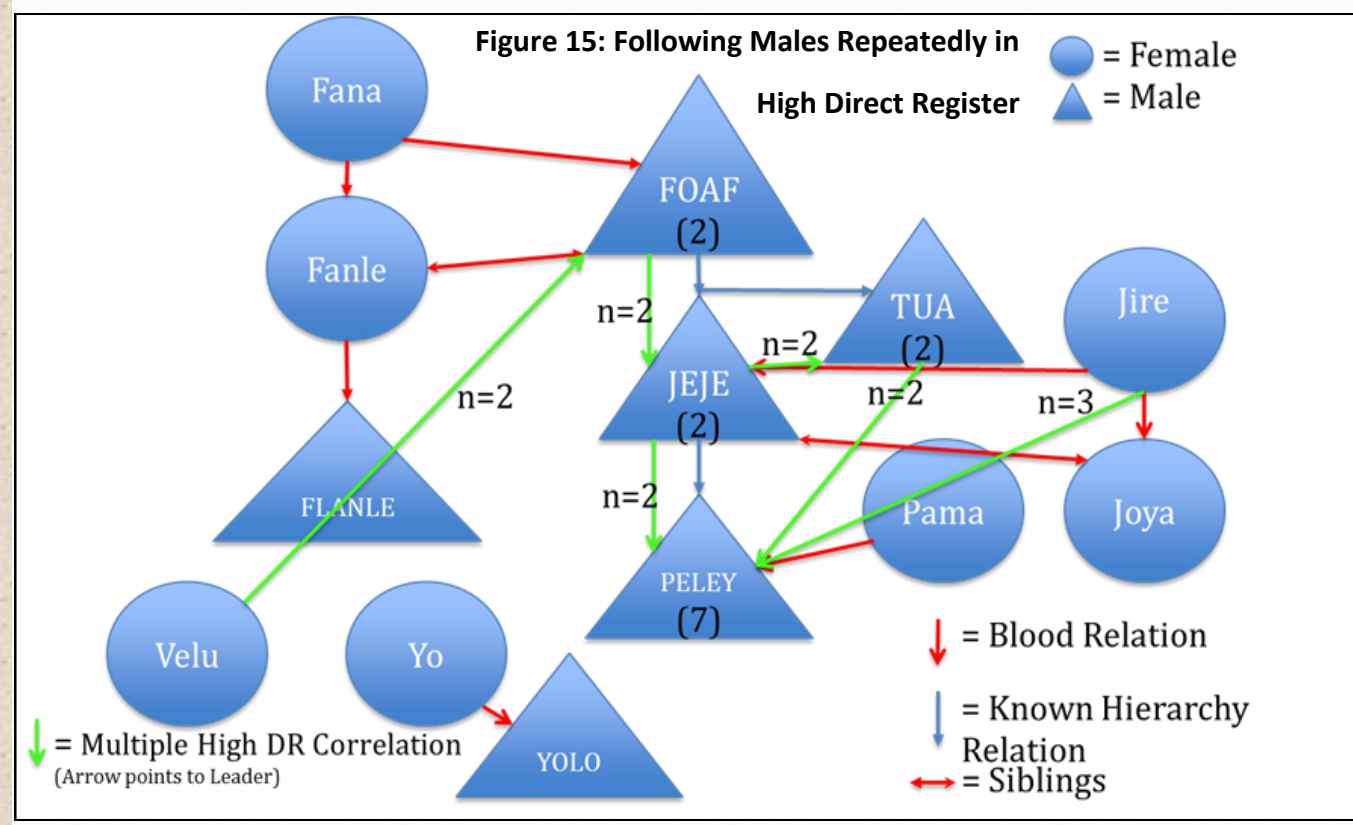
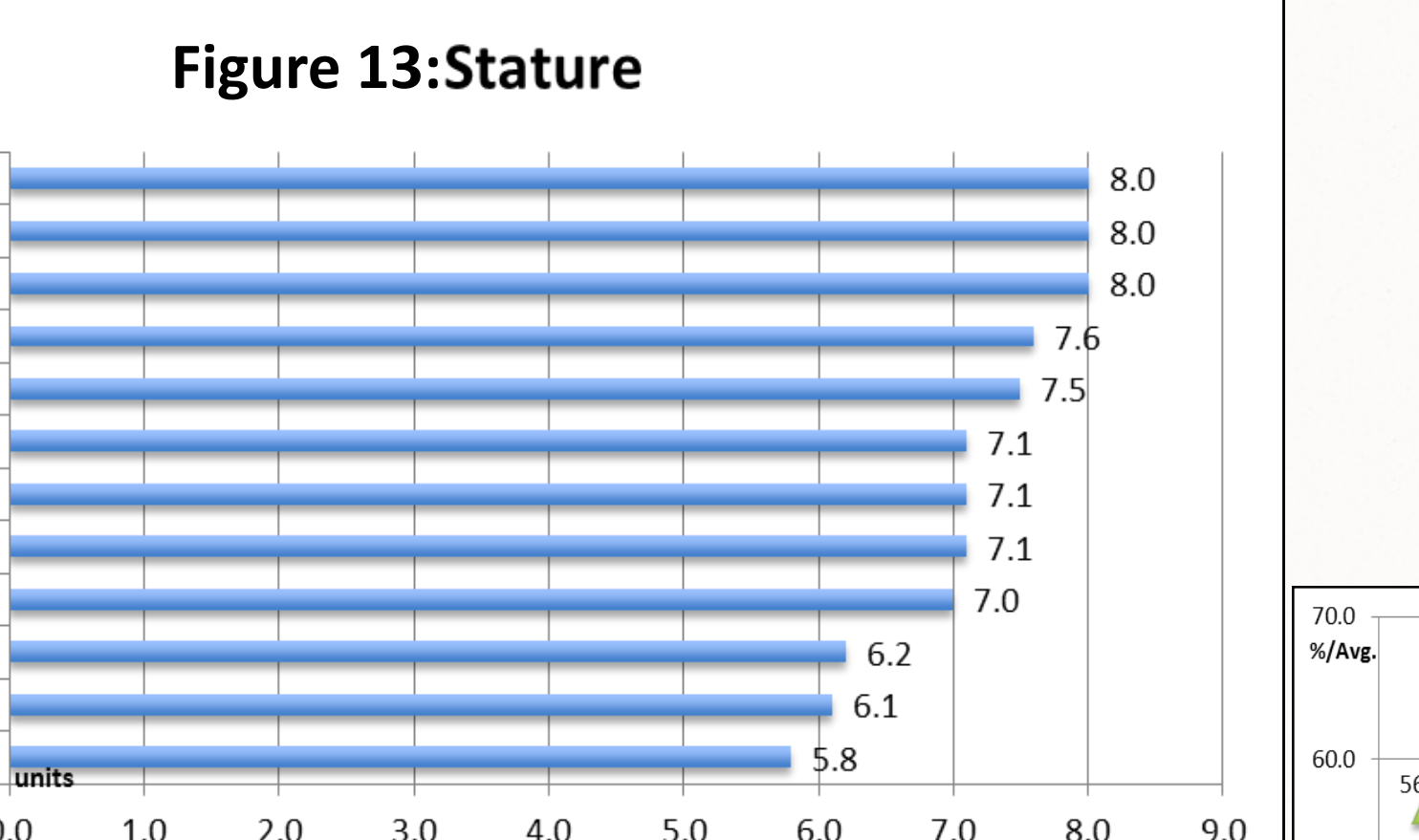
Sample Population: Twenty road crossing videos of chimpanzees from Guinea Bossou were analyzed for presence of direct register (Hockings and Yamamoto 2013). The total study population (n) was twelve, with group crossings ranging from four to eleven individuals. **Mapping:** Overlapping steps (So) of those where two individuals had both stepped (Sq) were highlighted with a green circle. Then the total number of overlapping steps were expressed in percent of direct register (So/Sq X 100). A physical separation number (Sep) between each individual was assigned (Black vs. Brown = 1, Black vs. Red = 2, etc.), and a comparison was done between all individuals involved in the road crossing to study proximity versus direct register percentage. **Stature Measurement:** To account for differences in height and stride, an assessment of stature was done between individuals in a group crossing. Similar stature should mechanically allow individuals a similar stride length, which would have a direct impact on the tendency of individuals to walk in direct register (Martin 2011). Stature was measured in arbitrary units from the ruler tool in Microsoft PowerPoint, and stated as a percentage of difference in stature between individuals. Stature was determined by overlaying a stick figure homunculus on a screen capture of each individual.

Results: Table 2 shows an average of 12.7 percent overlapping footsteps that were considered direct register walking. There were 69 instances where direct register was equal to or greater than 30 percent, which matched the low end average for the AMH studies. Thirteen pairs of individuals had repeat instances of direct register ranging from two to five occurrences. Six pairs of individuals produced percentages greater than 70 percent. The repeat and high percentage (>70 percent) data were examined more closely to tease out factors that contributed to producing moderately high direct register.

Proximity and Stature Results: Physical separation of three or less was used to define "close" proximity between individuals. Individuals ranged in stature from 5.8 to 8.0 units (Figure 13). When proximity and stature were compared to direct register percentage, stature difference was inversely proportional to direct register percentage, suggesting proximity between individuals was a more important factor than stature (Figure 14).

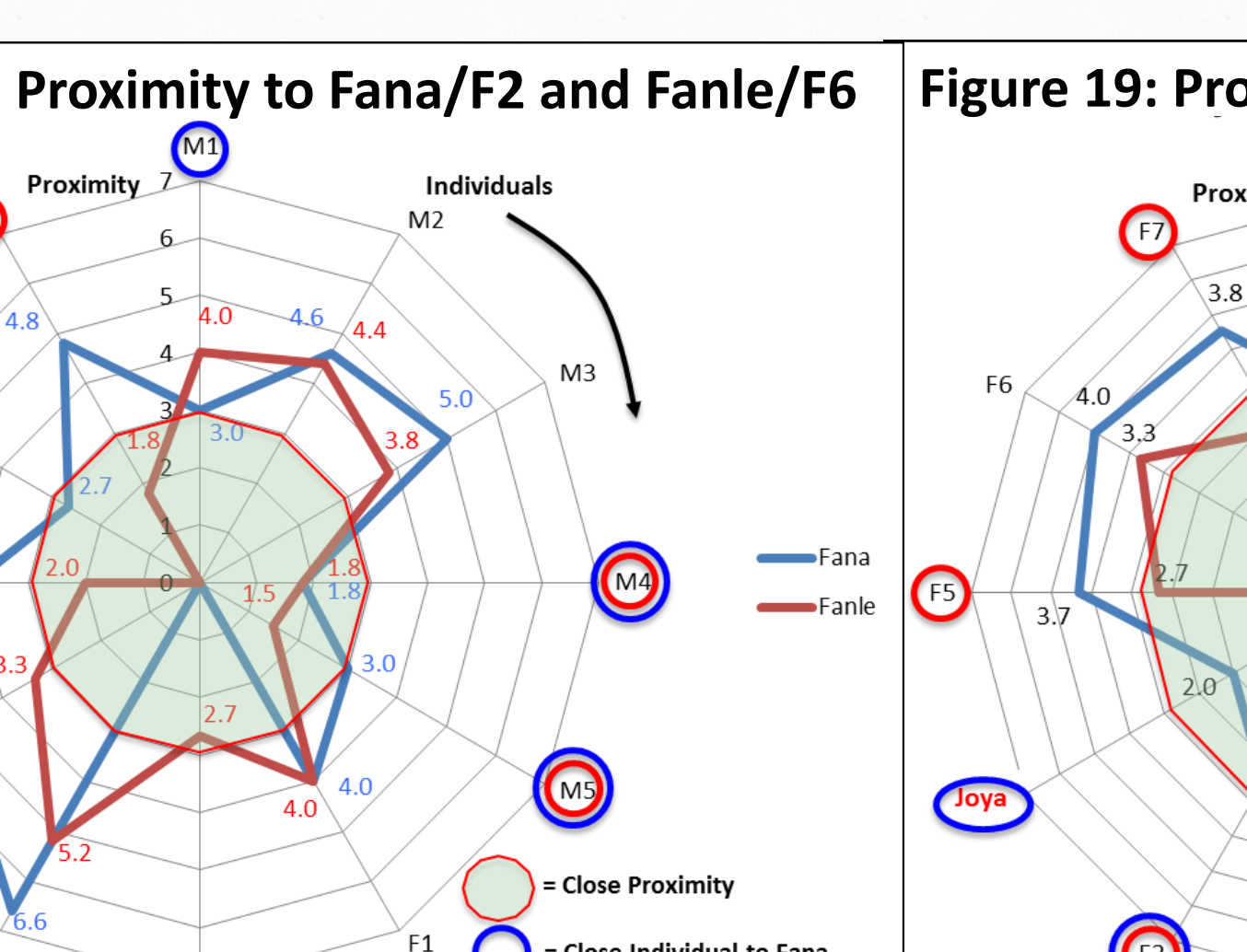
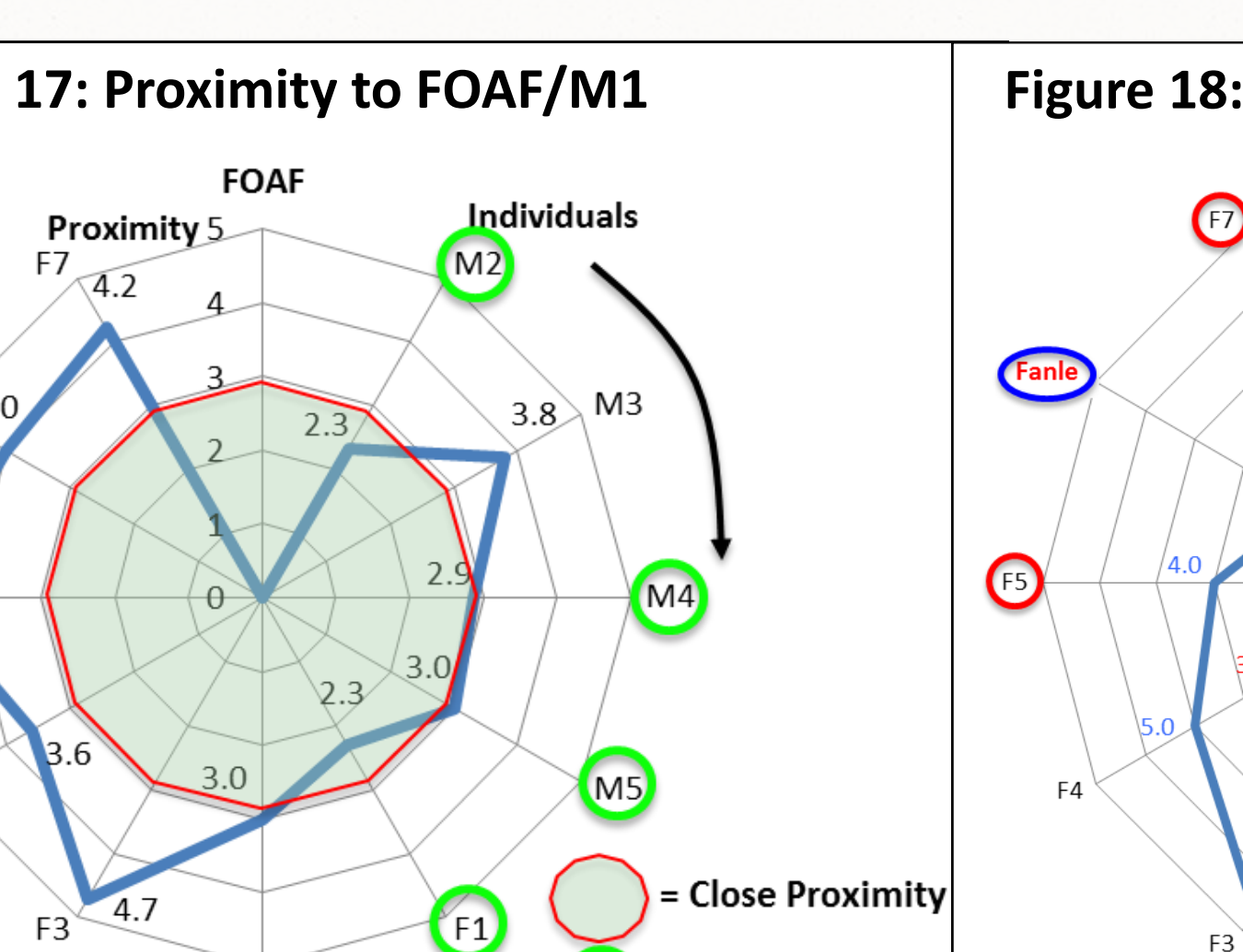
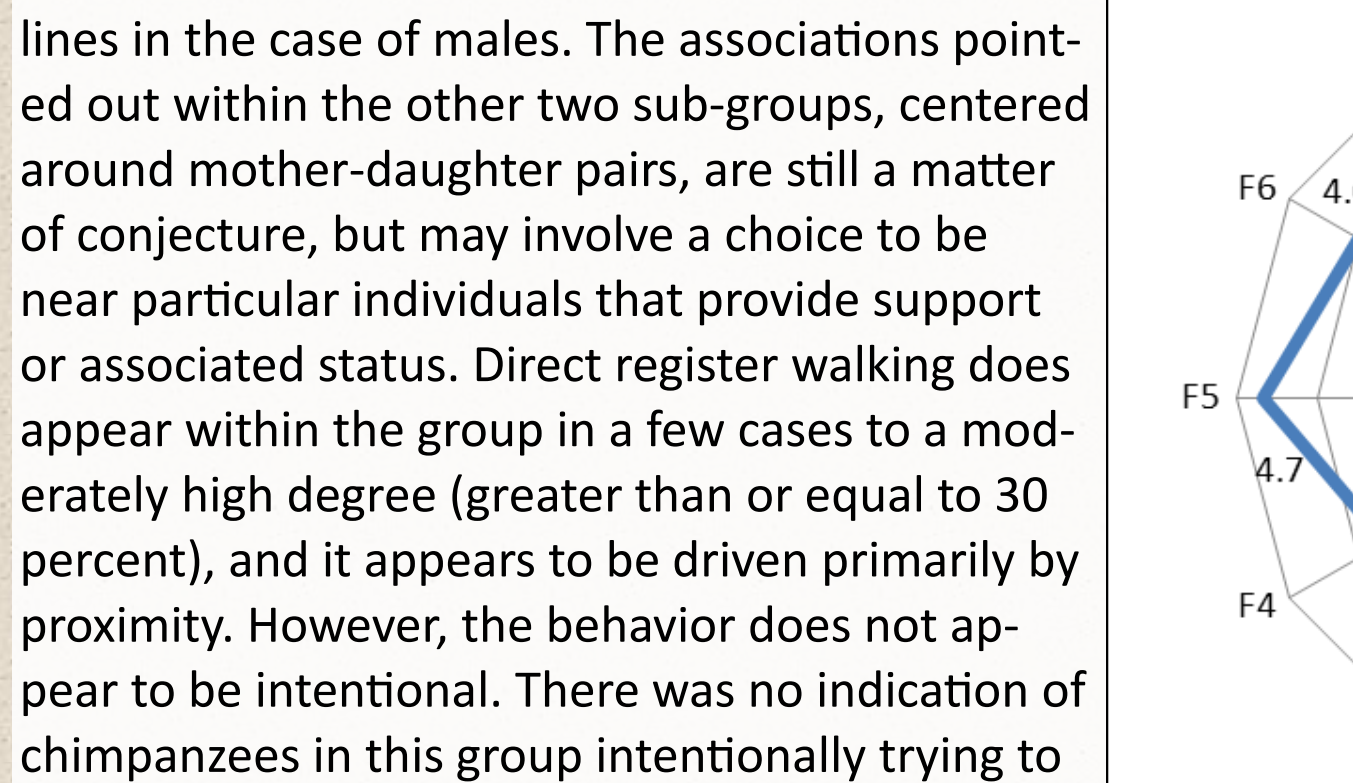
Social and Sex-based Makeup Results: Familial lineage and male hierarchy relationships were available for analysis for the Guinea Bossou group (Matsuzawa et al. 2011). These relationships are illustrated in Figures 15 and 16, and represent repeated occurrences of direct register between two individuals ≥ 30 percent by sex. When average proximity and multiple instances of moderately high direct register walking between individuals is examined in Figures 17-19, an interesting picture emerges regarding relationships and choices between different individuals in the group, especially females. All of the males except the beta male tend to stay in close proximity to the alpha male. In addition, the mothers of the alpha and beta males also stayed close to the alpha male. However, the two mothers do not stay close to each other, and they have cohorts made up of their daughters, and specific individuals that stay close to them and/or their daughters. There are two unknown status females who stay close to the daughters in each cohort, but not the mothers. Finally, there is one unknown status male (M5) who stays on the edge of every group, and who left the group after four road crossings during the original study period.

Video	n	Females	Males	Type	Risk	Road	Time on Road	Qualifying	Steps	Register (%)
20101223 (17)	10	6	4	Sm	H	1:10	1:11	88	8.6	
20101223 (18)	10	6	4	Lg	No	1:35	1:37	86	8.5	
20101227 (3)	8	4	4	Lg	No	0:37	0:45	67	8.2	
20101227 (4)	8	4	4	Sm	H, M	0:37	0:41	82	14.1	
20101231 (8)	8	4	4	Lg	No	0:50	0:51	59	8.7	
20101231 (9)	8	4	4	Sm	H	1:09	1:13	85	10.9	
20101002 (26)	10	6	4	Sm	H	0:50	0:58	117	18.3	
20101002 (27)	10	6	4	Lg	No	1:22	1:25	79	13.4	
20101007 (7)	8	5	3	Sm	H	0:30	0:33	69	10.0	
20101021 (14)	6	4	2	Lg	No	0:17	0:21	45	8.0	
20101021 (15)	7	3	4	Lg	No	0:30	0:32	76	13.5	
20101015 (8)	6	4	2	Lg	No	0:26	0:31	78	10.0	
20101017 (10)	6	4	2	Lg	M	0:30	0:32	49	11.9	
24.wmv	6	2	4	Lg	No	0:47	0:52	110	12.7	
24.wmv	11	6	5	Lg	H	1:01	1:07	132	5.2	
24.wmv	7	2	5	Sm	H	0:32	0:33	31	25.0	
14.3.wmv	7	2	5	Lg	No	1:07	1:08	63	26.1	
16.1.wmv	8	3	5	Msd	No	0:35	0:38	94	11.6	
24.2.wmv	9	4	5	Lg	H	0:24	0:24	43	21.4	
13.1.wmv	7	2	5	Lg	No	0:23	0:24	66	9.8	
Average	7.9	4.2	3.7			0:48	0:48	1519 (Avg)	12.7	
Std. Dev.	1.8	1.5	1.0			0:02	0:02		5.89	



Conclusions on Proximity: The data suggest that individuals do associate along familial lines in the case of mothers and daughters, and hierarchical lines in the case of males. The associations pointed out within the other two sub-groups, centered around mother-daughter pairs, are still a matter of conjecture, but may involve a choice to be near particular individuals that provide support or associated status. Direct register walking does appear within the group in a few cases to a moderately high degree (greater than or equal to 30 percent), and it appears to be driven primarily by proximity. However, the behavior does not appear to be intentional. There was no indication of chimpanzees in this group intentionally trying to walk in another individual's footsteps.

Directions for Further Research: My hope is that this study will expand to include different chimpanzee populations and terrain, such as video from different environments. Populations in savannah terrain, for example, could show group movement during long distance foraging. It would also be valuable to examine populations with patrolling behavior to see if intergroup violence is a factor in group movement.



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