

**Final Report for The Leakey Foundation:  
Japanese Macaques, Physical Disability and the Evolution of Conspecific Care**

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**Summary:**

The following report summarizes the findings from my PhD research on disability in free-ranging adult female Japanese macaques. In my research proposal, submitted to The Leakey Foundation in December 2005, I summarized my research questions as follows:

- (1) Do extant non-human primates provide care for physically disabled individuals? If so, what form does this care take, how might care-giving behaviors be explained from an evolutionary perspective, and what are the implications for the evolution of conspecific care in humans? and (2) Conversely, if non-human primates survive with extensive physical impairments without conspecific care, how is this accomplished, what are the costs, and what implications would this have for the evolution of conspecific care in humans?

Overall, I found little evidence for conspecific care for adult females with congenital limb malformations (CLMs), and this result lends support to the hypothesis that substantial conspecific care for disabled adults is a behaviour that differentiates ancestral and modern humans from nonhuman primates. However, I found considerable social “tolerance” for disabled individuals, that is, a neutral response to disability, which facilitates the survival of disabled monkeys and their participation in the social group. Such tolerance is a necessary, though not sufficient, condition for conspecific care. Also, in the free-ranging context at the Awajishima Monkey Center (AMC), where food was plentiful and predators were few, there was little evidence for social selection against disabled individuals. Results from this study also underscore the real *abilities* of the disabled monkeys at AMC; often in the literature on conspecific care in ancestral humans, researchers assume that disabled individuals would be unable to survive on their own [Lebel & Trinkaus, 2002; Lebel et al., 2001; Lordkipanidze et al., 2005] (for critique see [Cuzzo & Sauter, 2004; Dettwyler, 1991]). The results of my PhD research emphasize the importance of carefully examining such assumptions for individuals with even very extensive physical impairments; with behavioural flexibility and innovation, disabled adult female Japanese macaques were able to accomplish important social and life-sustaining behaviours such as grooming and feeding, without much or any apparent loss of functionality, depending on the behaviour. Also, disabled females did not appear to be more stressed, as

measured by fecal cortisol levels. In many cases, ancestral humans with disabilities may have been able to do well using their own abilities, without any special conspecific care or just with extra maternal care at specific life stages, such as during infancy, as we have previously observed with mother Japanese monkeys at Awajishima [Turner et al., 2005].

### **Publications and plans for publication:**

To date, results from this research project have been published in two papers:

Turner, Sarah E., Fedigan, Linda M., Nobuhara, Hisami, Nobuhara, Toshikazu, Matthews, H. Damon, Nakamichi, Masayuki. (2008) Monkeys with disabilities: Prevalence and severity of congenital limb malformations in *Macaca fuscata* on Awaji Island. *Primates*. 49(3), 223-226.

Turner, Sarah E., Fedigan, Linda M., Nakamichi, Masayuki, Matthews, H. Damon, McKenna, Katie, Nobuhara, Hisami, Nobuhara, Toshikazu, Shimizu, Keiko. (2010) Birth in free-ranging *Macaca fuscata*. *International Journal of Primatology*. 31:15-37. (see Appendix I)

I also wrote a science-based photographic storybook for children about Japanese macaques, in which The Leakey Foundation is acknowledged: Turner, Sarah E. (2010) *The Littlest Monkey*. Sono Nis Press, Winlaw B.C. ISBN 1-55039-174-7.

There are three more chapters of my dissertation [Turner, 2010] that I am currently preparing for submission:

1) Disability and social behaviour in free-ranging adult female Japanese macaques: conspecific care, tolerance or social selection against disability? (working title)

This paper is the heart of the study, and will deal primarily with the first research question listed above in the Summary section, an examination of the social context of disability and the possibility of conspecific care for disabled adult females.

2) Disability, compensatory behaviour and innovation in free-ranging adult female Japanese macaques (working title)

This paper will address the second question above, and will examine disability-associated behaviours in adult females.

3) Physical disability does not predict fecal cortisol levels in free-ranging Japanese macaques (working title)

This paper will also address part of the second research question described above and will examine cortisol and disability in the social context of these adult female Japanese macaques.

### **Description of Results:**

In conducting field research for this study, I examined the behavioural and physiological consequences of congenital limb malformations for adult females in a unique group of free-ranging Japanese macaques (*Macaca fuscata*) at the Awajishima Monkey Center, Japan. Previous research demonstrates that mothers provide extra care to disabled infants in the form of supported carrying and nursing; this care is vital for the survival of these infants with CLMs [Nakamichi, 1986; Turner et al., 2005]. However, data from my PhD research showed that

beyond infancy, there was little evidence for special conspecific care directed towards disabled adult females. Recognizing that this is a provisioned group, my results suggest that in addition to the benefits provided by the food-rich environment, disabled monkeys survived with sometimes extensive physical impairments from congenital limb malformations because of their ability to behave flexibly and find individual styles of locomotion, feeding and grooming, and because of the overall undifferentiated response among disabled and nondisabled individuals toward disabled monkeys, a tolerance and lack of social selection directed against disabled monkeys in the group. In many ways there were few differences between disabled and nondisabled adult females, in particular, time spent engaged in feeding and foraging and locomotion did not differ, and neither did their fecal cortisol levels, which are often interpreted as a measure of stress, and suggest that disabled females were not more stressed than their nondisabled counterparts.

I derived these results from behavioural and physiological data collected on 23 adult females, from 558 30-minute randomly ordered, continuous time focal animal follows and 569 fecal samples, collected over 3 birth seasons (May—August 2005, 2006 and 2007). Fecal samples were stored at  $-20^{\circ}\text{C}$  and cortisol analysis was conducted by Dr. Keiko Shimizu at the Kyoto University Primate Research Institute. I also collected *ad libitum* data, including detailed observations on two births that occurred in 2006 (see Appendix I).

In Turner et al. [2008], we presented the results of a pilot study, a census, conducted in 2004. It was necessary to gain an understanding of the number of disabled individuals in the group and the demographic characteristics of the group, in order to develop the main behavioural and physiological study of disability and to characterize the congenital limb malformations present and choose focal animals. We found that 17.1% of individuals had CLMs. Including previously published demographic data, we found that from 1969 to 2007, 16.1% of infants at AMC were born with CLMs, and many monkeys with even very extensive CLMs survive to adulthood and reproduce. We also developed an index to measure the extensiveness of individual CLMs, results of which I then used in my analyses of behavioural data. The percentage of disabled individuals at AMC is very high [Nakamichi et al., 1997; Yoshihiro et al., 1979], since rates of CLMs in primates are usually be well under 1% if any are reported at all [Brignolo et al., 2002; Morris, 1971]. In addition to issues that the situation at AMC raises in terms of human-environmental responsibility – the cause of CLMs remains unclear, although pesticides have been implicated [Ito et al., 1988] – the existence of the disabled monkeys at the AMC also afforded a unique opportunity to study disability in a free-ranging context with a relatively large sample of disabled adult primates.

There has been considerable debate over the years regarding the potential role of conspecific care for disabled individuals in ancestral hominins [Cuzzo & Sauther, 2004; DeGusta, 2002, 2003; Dettwyler, 1991; Holden, 2003; Lebel & Trinkaus, 2002; Lebel et al., 2001; Lordkipanidze et al., 2005; Millette et al., 2009]. Often the existence of conspecific care and the motivations for care, such as compassion, have been inferred from skeletal evidence of physical impairment. It is often assumed that the survival of disabled individuals depended on conspecific care and that such care was beyond that which would occur in modern nonhuman primates [Holden, 2003; Lordkipanidze et al., 2005]. However, since our knowledge of conspecific care behaviours in relation to disability in extant nonhuman primates has been very limited, such assumptions have mostly remained unsubstantiated [but see Cuzzo & Sauther, 2004]. The results of this study on free-ranging adult female Japanese macaques, however, generally support the hypothesis that

modern nonhuman primates do not engage in substantial conspecific care for disabled adults. However, results from this investigation reveal a complex individual and social portrait of disability at AMC and both the behavioural similarities among adult females and their disability-associated differences provide useful information for our understanding of disability in primates and the evolution of conspecific care in humans.

Results from this study showed that disabled female Japanese macaques rested significantly more and socialized significantly less compared to controls (Linear Mixed Effects Model in R [Crawley, 2007]: Rest:  $df = 21$ ,  $t$ -value = 3.803974,  $p$ -value = 0.0010; LME for Social:  $df = 21$ ,  $t$ -value = -3.152273,  $p$ -value = 0.0048) (Figure 1). This result was consistent across a number of measures: disabled females had fewer other monkeys in proximity at the start of focal follows (LME with data transformed by  $\log+1$ :  $df = 21$ ,  $t$ -value = -2.79503,  $p$ -value = 0.0108), fewer adult female affiliates per follow (LME with Poisson errors:  $z$ -value = -3.0669,  $p$ -value = 0.00216), less total passive social contact time (Kruskal-Wallis:  $\chi^2 = 4.6402$ ,  $df = 1$ ,  $p$ -value = 0.03123), fewer adult female grooming partners (LME with Poisson errors:  $z$ -value = -3.348,  $p$ -value = 0.000815), and spent less total time engaged in grooming with adult females (Kruskal-Wallis:  $\chi^2 = 2.9697$ ,  $df = 1$ ,  $p$ -value = 0.08484). Since disabled females were less social than their nondisabled counterparts, an important question in relation to conspecific care or conversely, social selection against disability, was who was driving the difference in social behaviour? Two measures, in particular, suggested that disabled females were responsible for reduced social involvement: disabled females were equally successful at soliciting grooming as nondisabled females and there was no difference in the ratio of disabled and nondisabled affiliates among focal animals, that is, there was no apparent preference related to the disability status of affiliates. It may be that accommodating CLMs has an energy cost for disabled individuals and that they reduce their social time and increase rest time to mitigate this cost.

Disabled females also received a lower frequency of intensive agonism (bite and chase) than controls (LME with Poisson errors:  $z$ -value = -2.047,  $p$ -value = 0.0407). However, Japanese macaques, particularly those in provision-fed groups, usually have a highly predictable social dominance hierarchy among females that is nearly entirely associated with kin relationships [Kawamura, 1958]. It is notable then that disabled females fell somewhat lower in the dominance hierarchy than expected according to kin relationships. Disabled females were not all low ranking, however, but overall, disabled females had a significantly greater difference between their observed and expected individual dominance rank than did nondisabled females (Kruskal-Wallis:  $df=19$ ,  $p$ -value=0.0076).

Overall, however, the statistically significant differences in social behaviour between disabled and nondisabled adult females suggest that there was little evidence for either conspecific care or social selection against disability. The data suggest that disabled monkeys themselves are at least partly responsible for their reduced sociality, and that overall, there is little evidence of social behavioural selection against disability in the Awajishima population. However, there is some evidence of a behavioural cost of disability; in particular, disabled adult females appear to have positions in the dominance hierarchy that are lower than expected. This suggests that disabled adult females may not be able to compete as well as nondisabled females, and are therefore losing rank to their nondisabled conspecifics. I did not observe any discernable, active conflicts over position among focal animals, and it seems likely that once a female's place in the hierarchy is established, it moves little. So, although results from this study suggest that there may be a rank-related cost associated with having CLMs, the lower-than-expected rank does not translate

into active social selection against disabled individuals. It is also possible that both the lower frequency of received intensive agonism and somewhat lower rank were manifestations of the overall reduced social behaviour of disabled females.

There was ample evidence among focal animals at AMC for tolerance and neutral response to disability. Although much is made of the modern human capacity for care for people with disabilities, the human response to disability is extremely varied, and has often been very negative [Berkson, 2004; Dettwyler, 1991]. It can be argued that a socially neutral response to disability, is a more caring response than occurs in many modern human contexts [Otake, 1998; Wendell, 1996]. In an evolutionary context, tolerance is little discussed, however, tolerance or a socially neutral response is a necessary though not sufficient condition for conspecific care to occur within a social context. At Awajishima a more-or-less neutral response to disability facilitated the social participation of disabled adult females, and allowed them to use their own behavioural flexibility to compensate for CLMs while remaining within the social group.

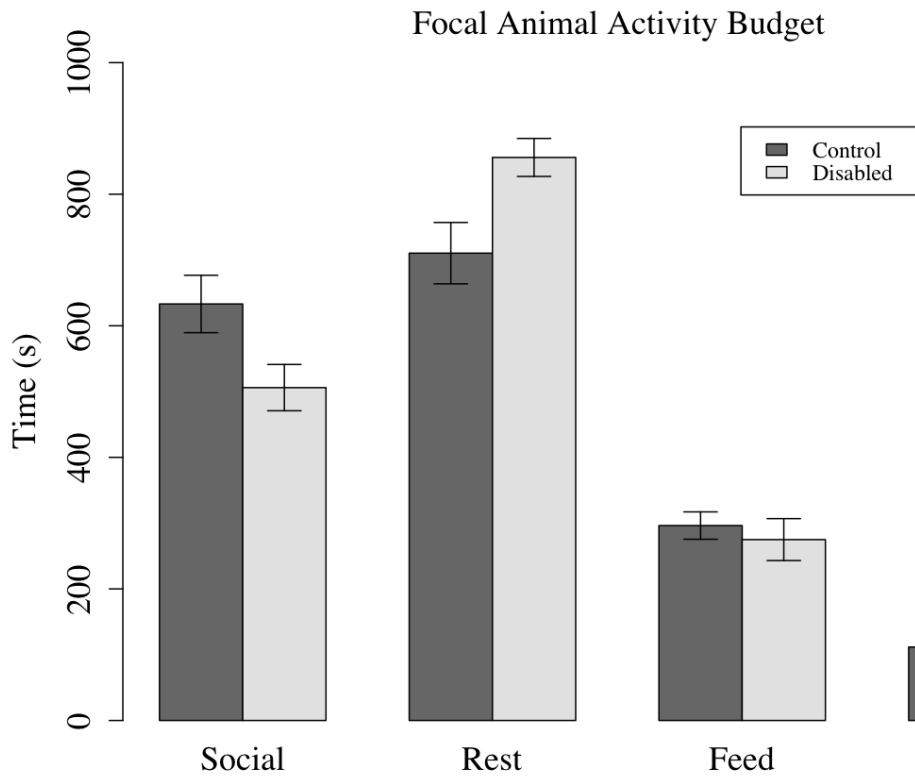
Since disabled adult females at AMC were living without disability-specific care from conspecifics, I examined how they were managing with sometimes extensive CLMs. Some disability-associated behavioural differences were immediately striking, such as habitual bipedalism and other locomotor variants used by some disabled animals. However some behavioural differences were more subtle, such as grooming technique, which also varied according to disability; disabled adult females showed lower frequency of hand use for removing louse eggs and compensated with increased direct use of the mouth and in some cases, a two-arm pinch technique (Figure 2) (hand use: Kruskal-Wallis: chi-squared = 7.6705,  $df = 1$ ,  $p = 0.005613$ ; mouth use: Kruskal-Wallis: chi-squared = 11.0455,  $df = 1$ ,  $p$ -value = 0.000889; two-arm pinch: Kruskal-Wallis: chi-squared = 4.2903,  $df = 1$ ,  $p$ -value = 0.03833). Self-scratching against substrates was almost exclusively a disability-associated behaviour (LME with Poisson distribution for Disability Index:  $z$ -value = 3.061,  $p$ -value 0.00220). I also observed innovative new ways of accomplishing some behaviours, for example, an extensively disabled female sometimes used her legs to pound the ground, disturbing invertebrates which she then caught with her mouth, while her nondisabled counterparts were pushing aside and sifting through the leaf litter with their hands to catch invertebrates. In many instances, disabled females were able to compensate behaviourally to perform social and life-sustaining activities, modifying existing behaviours to suit their individual physical situations and, occasionally, inventing new ways of doing things. In many ways, however, it was the similarity rather than the differences in behaviours among adult females that was most striking. For instance, physical impairment did not affect time spent feeding on provisioned and wild foods, nor did it affect overall terrestrial and arboreal use. And although, as discussed above, disabled females spent less time engaged in social behaviour, the overall pattern of their social lives was to a day to day observer, indistinguishable from that of nondisabled females: all focal animals engaged in social grooming, and spent time sitting in contact with and near other monkeys, cared for their offspring, and traveled with the group as they moved through the forest and to and from the provision feeding area at the AMC.

Another interesting similarity among focal animals was their levels of baseline fecal cortisol. Cortisol, a hormone released in response to stressors, has pathogenic effects when basal levels are chronically high, and therefore it provides a useful window into an organism's physiological

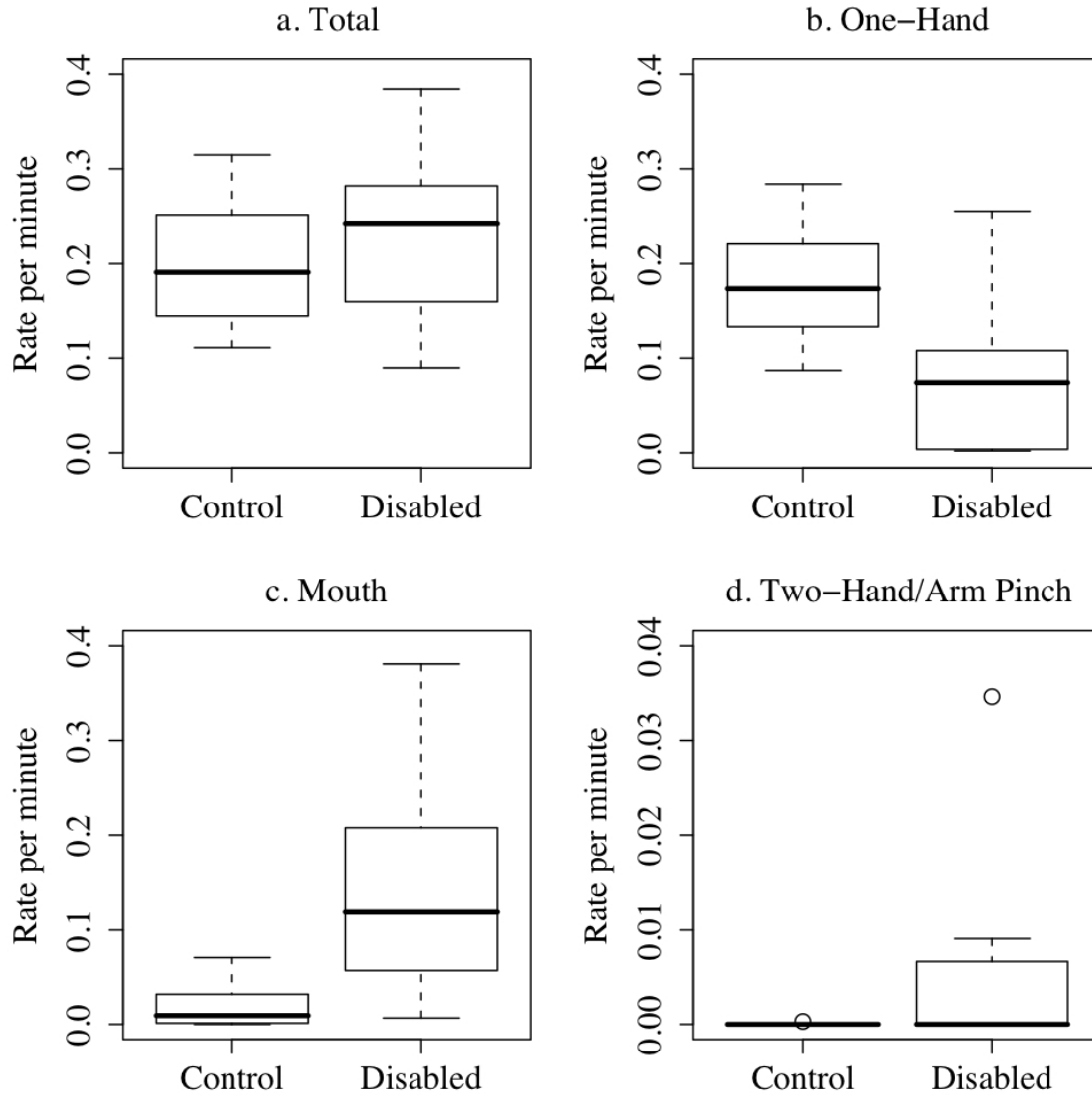
well-being[Sapolsky, 2002]. I explored the prediction that baseline cortisol levels would correlate positively with the presence and extensiveness of limb malformations in adult female Japanese macaques. In doing so, I examined a suite of variables known to relate to cortisol in other contexts, including: dominance rank [Abbott et al., 2003; Anestis, 2010; Sapolsky, 2005], exposure to predators [Engh et al., 2006], reproductive state [Hoffman et al., 2010; Sapolsky, 2005], rainfall [Behie et al., 2010], and availability of kin for social support[Abbott et al., 2003]. I also examined cortisol correlates of social behavioural variables. The frequency of intense received agonism correlated significantly and positively with cortisol levels. However, disability was not associated with cortisol levels, nor was exposure to predators (feral dogs), availability of social support or rainfall. Instead, relative dominance rank and study year had significant effects on cortisol, and reproductive state interacted significantly with year, although it was not significant on its own (LME relative rank:  $df = 18$ ,  $t$ -value = 2.165006,  $p$ -value 0.0441; LME year:  $df = 38$ ,  $t$ -value = -6.854928,  $p$ -value < 0.0000; LME reproductive state and year:  $df = 24$ ,  $t$ -value = -3.152056,  $p$ -value = 0.0043). These results point to the effectiveness with which disabled monkeys are able to behaviourally compensate for their CLMs, as well as the importance of social variables, such as dominance rank and agonism in influencing cortisol levels in free-ranging female Japanese macaques.

While, as discussed earlier, the results of this study generally support the hypothesis that modern nonhuman primates do not engage in substantial conspecific care for disabled adults, another relevant piece of the puzzle that emerged clearly from my results was that these disabled monkeys, even individuals with very extensive limb malformations, were able to compensate for their limb malformations and survive, reproduce and participate in the social milieu of the group. In a wild context, it is likely that not all of these individuals would have survived, but I think that many of them would survive, and survive better than would usually be assumed by nondisabled observers. Various researchers have pointed out that prejudice against people with disabilities leads to assumptions about what people with disabilities are actually capable of [Otake, 1998]. When developing arguments about whether or not an ancestral hominin individual could have survived without conspecific care with a particular antemortem skeletal lesion, the potential abilities of disabled individuals in ancestral hominins should not be underestimated.

Overall, I found that focal animals with CLMs were able to compensate with behavioural flexibility and innovation, including modifying activity budgets to include more rest and less social activity, employing individual styles of locomotion, and utilizing the mouth and a unique two-hand pinch method in grooming. Notably, disabled monkeys did not differ from controls by a number of measures, including time spent feeding and foraging, speed of locomotion, canopy usage, and stress, as measured through fecal cortisol levels. The only consistent predictor of fecal cortisol concentrations was relative social dominance, such that subordinate females had higher cortisol than dominant females. I found little evidence for conspecific care directed towards disabled adult females. However there was also little evidence for social selection against disability. The differences in social behaviour appeared to be primarily driven by the disabled monkeys themselves, in the context of a group that showed an overall undifferentiated response to disabled and nondisabled adult females, tolerance that helped facilitate the survival of disabled monkeys at AMC.



**Figure 1** Activity budgets for disabled and nondisabled focal animals. There are significant differences between disabled monkeys and controls for total time spent engaged in social activities and total time spent resting. There were no significant differences associated with total feeding time or total time spent traveling. Time is shown in seconds and is average time per 30-minute focal animal follow. (The remainder of the 30 minutes is taken up with other activities and out-of-sight time, neither of which are significant and are not shown) [from Turner, 2010].



**Figure 2** Boxplots of mean rates of grooming method use per minute of grooming time (in which visibility was adequate to count hand-to-mouth and mouth-to-body motions); a) total rate of all methods used; b) rate of one-handed pick-up of louse egg or debris to bring it to the mouth; c) rate of direct mouth-to-skin contact; d) rate of use of two-hand/arm pinch to bring louse egg or debris to the mouth. Note that the y-axis scale in plot (d) is much smaller than the others. In the boxplot, the thicker horizontal line inside the box shows the median value. The top and bottom of the box show the first and third quartiles (the 25<sup>th</sup> and 75<sup>th</sup> percentiles). The differences between the top and bottom lines is the interquartile range. If there are no outliers, then the dashed vertical lines show the maximum and minimum values for the data. If there are outliers, they are represented by the open circles, and in this case, the dashed vertical lines show 1.5 times the interquartile range, or approximately 2 standard deviations [Crawley, 2007] [from Turner, 2010].

**Appendix I: Birth in Japanese macaques:**

In Turner et al. [2010], we presented the results of another investigation, a side project in relation to the main study of disability in adult females, but research with relevance to human evolution nonetheless. During the 2006 field season, we were lucky enough to observe two births that occurred during the day at the Awajishima Monkey Center. Detailed, quantitative descriptions of parturition in nonhuman primates are still relatively rare. Observations of free-ranging births can help to elucidate factors involved in this critical event, to contribute to our understanding of how maternal and infant behaviours during parturition affect infant survival, and to explain the evolution of human birth. We presented data on the parturition behaviour of four multiparous Japanese macaques: two daytime live births that we photographed and were video recorded at the Awajishima Monkey Center (AMC), Awaji Island, Japan in 2006; a daytime live-birth video recorded in 1993 at the AMC [H Nobuhara and T Nobuhara, unpublished data]; and a captive *M. fuscata* nocturnal breech stillbirth, video recorded at the Kyoto University Primate Research Institute in 2006 [K Shimizu, unpublished data]. Certain behaviours were similar among the females, such as touching of the vulva followed by licking of fingers, squatting during contractions, and average contraction durations. Parturient females facilitated the birth manually by guiding the emerging infant. There were also dissimilarities in terms of the duration of the labour and birth stages, condition of the infant at birth, and the mother's behaviour immediately postpartum. The mothers' postpartum behaviours ranged from almost entirely infant-focused to predominantly related to the consumption of the placenta. The three free-ranging females all showed considerable social tolerance during labour and birth. Human birth is unique among primates in terms of the level of assistance that is normally provided to the parturient woman, and it has been argued that social involvement in birth evolved in humans because of relatively tight maternal-pelvic opening size to fetal cranial size ratio in humans, a result of bipedalism and encephalization [Rosenberg & Trevathan, 2002]. However, based on our observations of the Japanese macaques at Awajishima and a survey of the primate literature, we argued that social proximity at parturition is more common in nonhuman primates than has been previously emphasized. We argued that social proximity has potential adaptive advantages that may have shaped the evolution of social behaviour in human and nonhuman primate birth; these advantages include reduced predation risk that likely accompanies birthing in close proximity to the group, with more individuals to spot predators as well as more targets for those potential predators, and kinselection, since it seems likely that young females who have observed births would be more likely to react favorably to the birth of their own first infant.

**References:**

1. Abbott DH, Keverne EB, Bercovitch FD, Shively CA, Medoza SP, Saltzman W, Snowdon CT, Ziegler TE, Banjevic M, Garland T, Jr., Sapolsky RM. 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior* 43:67-82.
2. Anestis SF. 2010. Hormones and social behavior in primates. *Evolutionary Anthropology* 19:66-78.
3. Behie AM, Pavelka MSM, Chapman CA. 2010. Sources of variation in fecal cortisol levels in howler monkeys in Belize. *American Journal of Primatology* 72:600-606.
4. Berkson G. 2004. Intellectual and physical disability in prehistory and early civilization. *Mental Retardation* 42(3):195-208.
5. Brignolo L, Tarara R, Peterson PE, Hendrickx AG. 2002. Two cases of digital defects in *Macaca mulatta* infants and a survey of the literature. *Journal of Medical Primatology* 31:98-103.
6. Crawley MJ. 2007. *The R Book*. London, UK: Imperial College London at Silwood Park.
7. Cuozzo FP, Sauther ML. 2004. Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): Implications for inferring conspecific care in fossil hominids. *Journal of Human Evolution* 46:623-631.
8. DeGusta D. 2002. Comparative skeletal pathology and the case for conspecific care in middle pleistocene hominids. *Journal of Archaeological Science* 29:1435-1438.
9. DeGusta D. 2003. Aubesier 11 is not evidence of neanderthal conspecific care. *Journal of Human Evolution* 45:91-94.
10. Dettwyler KA. 1991. Can paleopathology provide evidence for "compassion"? *American Journal of Physical Anthropology* 84:375-384.
11. Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL. 2006. Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society of London Series B: Biological Sciences*(273):707-712.
12. Hoffman CL, Ayala JE, Mas-Rivera A, Maestriperi D. 2010. Effects of reproductive condition and dominance rank on cortisol responsiveness to stress in free-ranging rhesus macaques. *American Journal of Primatology* 72:559-565.
13. Holden C. 2003. Neanderthals not caring? *Science* 301:1319.
14. Ito M, Ogawa K, Sonobe T, Nakaminami G, Ishida N, Watanabe N, Inagaki H, Nigi H. 1988. Relation of the congenital limb malformation in the Japanese monkey on organochlorine pesticide. *Primate Research* 4:103-133.
15. Kawamura S. 1958. The matriarchal social order in the Minoo-B group. *Primates* 1(2):149-156.
16. Lebel S, Trinkaus E. 2002. Middle Pleistocene human remains from the Bau de l'Aubesier. *Journal of Human Evolution* 43:659-685.
17. Lebel S, Trinkaus E, Faure M, Fernandez P, Guérin C, Richter D, Mercier N, Valladas H, Wagner GA. 2001. Comparative morphology and paleobiology of middle Pleistocene human remains from the Bau de l'Aubesier, Vaucluse, France. *Proceedings of The National Academy of Sciences of The United States of America* 98:11097-11102.
18. Lordkipanidze D, Vekua A, Ferring R, Rightmire GP, Auusti J, Kiladze G, Mouskhelishvili A, Nioradze M, Ponce de Leon MS, Tappen M, Zollikofer CPE. 2005. The earliest toothless hominin skull. *Nature* 434:717-718.
19. Millette JB, Sauther ML, Cuozzo FP. 2009. Behavioral responses to tooth loss in wild ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly special reserve, Madagascar. *American Journal of Physical Anthropology* 140:120-134.
20. Morris LN. 1971. Spontaneous congenital limb malformations in nonhuman primates: Review of the literature. *Teratology* 4:335-342.
21. Nakamichi M. 1986. Behavior of infant Japanese monkeys (*Macaca fuscata*) with congenital limb malformations during their first three months. *Developmental Psychobiology* 19:335-341.

22. Nakamichi M, Nobuhara H, Nobuhara T, Nakahashi M, Nigi H. 1997. Birth rate and mortality rate of infants with congenital limb malformations of the limbs in the Awajishima free-ranging group of Japanese monkeys (*Macaca fuscata*). *American Journal of Primatology* 42:225-234.
23. Ototake H. 1998. No one's perfect. Harcourt G, translator. Tokyo: Kodansha International.
24. Rosenberg K, Trevathan W. 2002. Birth, obstetrics and human evolution. *BJOG: an International Journal of Obstetrics and Gynaecology* 109:1199-1206.
25. Sapolsky RM. 2002. Endocrinology of the stress response. In: Becker JB, Breedlove SM, Crews D, McCarthy M, editors. *Behavioral endocrinology*. Second ed. Cambridge Mass: MIT Press. p 409-450.
26. Sapolsky RM. 2005. The influence of social hierarchy on primate health. *Science* 308(5722):648-652.
27. Turner SE. 2010. Consequences of congenital limb malformations and disability in adult female Japanese macaques (*Macaca fuscata*) [Dissertation]. Calgary AB: University of Calgary. 229 p.
28. Turner SE, Fedigan LM, Nakamichi M, Matthews HD, KcKenna K, Nobuhara H, Nobuhara T, Shimizu K. 2010. Birth in free-ranging *Macaca fuscata*. *International Journal of Primatology* 31(1):15-37.
29. Turner SE, Fedigan LM, Nobuhara H, Nobuhara T, Matthews HD, Nakamichi M. 2008. Monkeys with disabilities: Prevalence and severity of congenital limb malformations in *Macaca fuscata* on Awaji island. *Primates* 49(3):223-226.
30. Turner SE, Gould L, Duffus DA. 2005. Maternal behavior and infant congenital limb malformation in a free-ranging group of *Macaca fuscata* on Awaji island, Japan. *International Journal of Primatology* 26(6):1435-1457.
31. Wendell S. 1996. *The rejected body: Feminist philosophical reflections on disability*. New York: Routledge.
32. Yoshihiro S, Goto S, Minezawa M, Muramatsu M, Saito Y, Sugita H, Nigi H. 1979. Frequency of occurrence, morphology, and causes of congenital malformation of limbs in the Japanese monkey. *Ecotoxicology and Environmental Safety* 3:458-470.