RESEARCH ARTICLE

Disability, Compensatory Behavior, and Innovation in Free-Ranging Adult Female Japanese Macaques (*Macaca Fuscata*)

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Little is known about consequences of disability in nonhuman primates, yet individuals with disabilities can reveal much about behavioral flexibility, innovation, and the capabilities of a species. The *Macaca fuscata* population surrounding the Awajishima Monkey Center has experienced high rates of congenital limb malformation for at least 40 years, creating a unique opportunity to examine consequences of physical impairment *in situ*, in a relatively large sample of free-ranging adult monkeys. Here we present behavioral data on 11 disabled adult females and 12 nondisabled controls from 279 hours of randomly ordered 30-minute focal animal follows collected during May–August in 2005, 2006, and 2007. We quantified numerous statistically significant disability-related behavioral differences among females. Disabled females spent less time begging for peanuts from tourists, and employed a behavioral variant of such peanut begging; they had a lower frequency of hand use in grooming and compensated with increased direct use of the mouth or a two-arm pinch technique; and they had a higher frequency of self-scratching, and more use of feet in self-scratching. Self-scratching against substrates was almost exclusively a disability associated behavior. Two females used habitual bipedalism. These differences not withstanding, disabled females behaved similarly to controls in many respects: overall reliance on provisioned and wild foods, time spent feeding, and feeding efficiency did not differ among females, and there was no time difference in behavior performed arboreally or terrestrially. Disabled adult females were able to compensate behaviorally to perform social and life-sustaining activities, modifying existing behaviors to suit their individual physical situations and, occasionally, inventing new ways of doing things. Am. J. Primatol. 74:788–803, 2012. © 2012 Wiley Periodicals, Inc.

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INTRODUCTION

Rates of congenital limb malformations (CLMs) in the population of free-ranging *Macaca fuscata* at the Awajishima Monkey Center (AMC) on Awaji Island, Japan, have been unusually high since the 1960s [Homma, 1980; Nakamichi et al., 1997; Turner et al., 2008; Yoshihiro et al., 1979]. In a 2004 census of the provisioned population, 17.1% of the monkeys had CLMs, and from 1969 to 2007 at least 185 individuals with CLMs were born, with an average of 16.1% of infants born with CLMs in any given year [Turner et al., 2008]. Survival in the first year of life is not as high for infants with CLMs as for those without, however, Nakamichi and colleagues [1997] found that 71.8% of infants with CLMs survived their first year, and many survive to adulthood. While longevity and fitness are likely negatively impacted by CLMs beyond the first year of life as well, the consistent availability of high quality provisioned food, mostly accessible through scramble (not direct) competition, likely improves the survival of disabled individuals from what it would be under wild conditions, and likely helps offset fitness costs of physical impairment (S.E. Turner and

colleagues, unpublished data). The cause of these CLMs in Japanese macaques is unclear, although genetic and environmental factors have been suggested [Homma, 1980; Ito et al., 1988; Minezawa et al., 1990; Morris, 1971; Yoshihiro et al., 1979]. Regardless of etiology, however, little has been documented about the consequences of physical impairment and disability in wild and free-ranging primates, particularly for adult monkeys. This study examines the behavior of adult females with CLMs, building on pervious research that focused on infants and disability and maternal behavior toward disabled infants [Nakamichi et al., 1983a; Nakamichi et al., 1983b; Turner et al., 2005].

Carey and colleagues [2007 identified and outlined some overarching principles of disability using *Drosophila* as a model. They concluded that: (1) impairments increase mortality risk, (2) multiple impairments have a synergistic negative effect on survival, (3) effects of impairment are contingent on the individual's environment, and (4) the effects of impairment are age and sex specific. While informative, the *Drosophila* model does not account for social interactions or individual behavioral flexibility and innovations that may compensate for or exacerbate the effects of disability (S.E. Turner and colleagues, unpublished data), the types of interactions that are recognized in the World Health Organization definition of disabilities. The WHO defines disability, in part, as a "complex phenomenon, reflecting an interaction between features of a person's body and features of the society in which he or she lives" (WHO, 2001, http://www.who.int/topics/disabilities/en/). The potential for injury, illness, and physical impairment is part of life for all animals, and skeletal evidence shows hominin individuals with chronic impairments from as early as 1.77 million years ago [Lebel and Trinkaus, 2002; Lordkipanidze et al., 2005]. There are also examples of nonhuman primate individuals who have survived with long-term disabilities in the form of antemortem tooth loss, injury-induced manual disability, and CLMs [Berkson, 2004; Chapman and Chapman, 1987; Cuozzo and Sauther, 2004; Fedigan and Fedigan, 1977; Nakamichi et al., 1983a; Nakamichi et al., 1983b; Nakamichi et al., 1997; Turner et al., 2005; Turner et al., 2008].

Considerable attention in the literature has been devoted to the innovation of new behaviors, individual and social learning, social traditions, and behavioral flexibility [Drapier and Thierry, 2002; Fragaszy and Perry, 2003; Huffman and Hirata, 2003; Huffman and Quiatt, 1986; Kawai, 1965; Leca et al., 2008]. Nonhuman primates have shown a sometimes remarkable ability to compensate behaviorally for physical impairments, offsetting potential costs of disability [Byrne and Stokes, 2002; Kummer and Goodall, 1985; Millette et al., 2009; Stokes,

1999; Stokes and Byrne, 2001]. When an animal is ill, injured, or disabled, the usual daily behaviors that sustain life, growth, and reproduction may no longer be possible or may not suffice, and individuals may be pushed, by necessity, to innovate and implement new behaviors or behavior patterns, or to adapt existing behaviors [Kummer and Goodall, 1985]. Examining the behavior of monkeys with CLMs—ordinary animals in unusual circumstances, animals who may be pushed by their physical circumstances beyond the usual repertoire of species-typical behavior—can reveal much about behavioral flexibility, resiliency, behavioral innovation, and the capabilities of a species [Arlet et al., 2009; Chapman and Legge, 2009; Stokes, 1999; Stokes and Byrne, 2001].

Injury, illness, and disability can impact individual growth, reproduction, and survival [Berkson, 2004; Carey et al., 2007; Lovell, 1991]. While injury is relatively common in primates [Arlet et al., 2009; Chapman and Chapman, 1987; Chapman and Legge, 2009; Dittus and Ratnayeke, 1989; Kano, 1984], the number of individuals affected by long-term physical disabilities is generally low in most primate populations. For instance, rates of congenital limb malformation are usually well under 1% if any occurrences are reported at all [e.g., Hendrickx and Prahalada, 1986; Peterson et al., 1997; Rawlins and Kessler, 1983]. In addition to the Awajishima *M. fuscata* population, there are a couple of notable exceptions: some populations of chimpanzees and bonobos have high rates of physical impairment caused by snare injuries [Byrne and Stokes, 2002; Kano, 1984; Quiatt et al., 2002; Stokes, 1999; Stokes and Byrne, 2001; Waller and Reynolds, 2001]; and recent studies on ring-tailed lemurs suggest that survival with serious dental impairment may be more common than previously thought, at least for this species [Cuozzo and Sauther, 2004; Millette et al., 2009]. These examples notwithstanding, the situation at AMC provides an uncommon opportunity to examine physical impairment noninvasively and *in situ*, in a relatively large sample of free-ranging adult nonhuman primates.

Research has shown that disability can influence feeding behaviors in primates. For instance, in relation to injuries, *Macaca sinica* were found to rest and groom more, and feed less, while injuries were healing compared to once they had healed [Dittus and Ratnayeke, 1989]. On the other hand, *Lemur catta* with dental impairment, engaged in more feeding time during a period of the day when others tended to rest [Millette et al., 2009]. In addition, disability can also impact the details of behavioral processes and techniques, such as occurs when great apes modify food processing procedures [Byrne and Stokes, 2002; Stokes, 1999; Stokes and Byrne, 2001]. Furthermore, physical impairment has potential consequences for locomotor ability. CLMs can

affect manual functionality, dexterity, and the ability to grasp objects. Hands are normally used to perform many life-sustaining activities; in addition to feeding and climbing, hands are usually used for both auto and allogrooming, behaviors that are important socially and in terms of reduction of ectoparasite burdens [Nakamichi and Shizawa, 2003; Tanaka, 1995; Tanaka and Takefushi, 1993; Yamada et al., 2005].

In this article, we will address the following questions and hypotheses: (1) How do CLMs influence the behavior of adult female Japanese macaques, particularly in relation to feeding and locomotion? We tested the following hypotheses: (i) disabled females would rely more on provisioned foods than nondisabled females, spending more time provision feeding than nondisabled females; (ii) disabled females would not feed as efficiently as nondisabled females; (iii) disabled females would locomote more slowly than nondisabled females, spending less time running, and more time walking; and (iv) disabled females would spend less time in the canopy overall, and especially less time in the high canopy (>10 m). (2) How do adult female Japanese macaques with CLMs compensate for physical impairment? We expected that disabled females would compensate for their disabilities in a variety of ways indicative of behavioral flexibility and innovation. We expected to quantify habitual bipedalism among some disabled females. We predicted that disabled females would modify behaviors that usually require four limbs and/or precise hand use. We tested the following hypotheses: (v) disabled females would use different grooming techniques from nondisabled females, in particular, we expected to see more use of the mouth and unusual patterns of hand usage; (vi) disabled females would use different techniques associated with self-scratching; and (vii) disabled females would use different feeding techniques than nondisabled females. We were also expecting to see other disability associated behaviors, including potentially, the innovation of novel solutions to individual disability challenges. (3) What are the adaptive implications of disability associated behavioral flexibility and innovation? In relation to this third question, we discuss our findings in terms of the adaptive implications of behavioral flexibility and innovation in the context of physical disability.

METHODS

All data collection was noninvasive and complied with the requirements of the University of Calgary Animal Care Committee and those of the AMC in Japan, the research adhered to the legal requirements in Japan and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates.

Study Subjects

Study subjects included 23 free-ranging adult female Japanese macaques living near the Awajishima Monkey Center on Awaji Island, Japan. There were about 200 *M. fuscata* living primarily in one large multimale, multifemale social group in the forest surrounding the AMC, with some peripheral all-male groups in the area as well. In a census in 2004, we identified 34 individuals with some level of CLM, of whom 13 were adult females [Turner et al., 2008]. We selected adult females as focal animals because of our continued interest in mother–infant interactions, in order to have the largest possible sample size of substantially disabled individuals while controlling for life-stage and sex, and because there is very little known about how long-term disability influences adult primates.

The main group usually visits the provision feeding area twice a day for regular feedings of wheat, soy beans, and some fruit from November to August. They are also fed peanuts through a wire enclosure by tourists throughout the day. The focal animals included all substantially disabled adult females in the group (2005–2007) (Table I) and controls, pair-matched to the disabled animals, first by kinship, and secondarily by age and estimated rank for those with unknown kin relationships or for those without available relatives.

Data Collection

We collected data over three consecutive birth seasons (May–August; 2005, 2006, and 2007); the data set included 279 hours of behavioral data using 30-minute continuous time focal animal sampling [Altmann, 1974], with no more than 5 minutes out-of-sight time per follow. Sampling order was determined by a random draw without replacement, and we endeavored to sample each animal once before beginning the next round of sampling, in this way we ensured that we had the same number of samples per individual per year, collected at similar intervals. We made two systematic deviations from the random order: (1) if we could not locate a monkey within 15 minutes, we moved to the next available on the list, and (2) in heavy rain, the monkeys tended to huddle inactively, so we limited the number of focal animals follows per individual during heavy rainfall in order to control for weather-related behavioral variation within the sample.

Behavioral data were collected on hand-held Palm devices (Tungsten E with an auxiliary minikeyboard, and Tungsten C) using a data collection program written for this study (J. Ha, unpublished program).

Analyses

At the end of each field day, we uploaded the data into Excel (version X for Mac and 2004 for PC).

TABLE I. Details of Focal Animal Congenital Limb Malformations

Female ID	Year born	Index[a]	CLM details[b]
Fumin	1996	0.33	Both hands; RH & LH 2, 3, & 4 absent, 1 & 5 and hands malformed
Kinchan	1995	0.28	Both hands; RH 1,3, & 4 absent, 2 & 5 and hand malformed, LH 3 & 4 absent, 2 & 5 and hand malformed
Kobato	1993	0.43	Both hands and both feet; RH 1, 2, 3, & 4 absent, 5 malformed, hand mostly absent; LH 2, 3, & 4 absent, 1 & 5 malformed, hand malformed; RF & LF 2 malformed, 3 absent
Nachan	1995	0.13	Both hands; RH 3 malformed, 3 absent; LH 3 absent, 2 & 4 malformed
Pikaru	1992	0.56	Both hands and both feet; RH and LH 1, 2, 3, & 4 absent, 5 and hands malformed, RF 2 & 3 absent, 1 and foot malformed, LF 2 & 3 absent, 1, 4, &5 and foot malformed
Punch	1998	0.38	Both hands and R foot; RH 1, 3, 4, & 5 absent, 2 malformed and hand essentially absent; LH 1, 2, 3, & 4 absent, 5 malformed and hand essentially absent, RF small extra digit
Ran	1991	0.24	Both hands and L foot; RH 3 absent, 2 & 4 malformed; LH 3 & 4 absent, 2 & 5 and hand malformed; LF 2 & 3 absent, 1 and foot malformed
Ribbon[c]	2001	0.72	Both arms and both feet; RH and LF entirely absent, elbows lacking mobility; RF 1, 2, & 3 absent, 4 & 5 and foot malformed; LF 1, 2, 3, & 4 absent, 5 and foot malformed
Wendy	1999	0.37	Both hands and both feet; RH 3 & 4 absent, 5 and hand malformed; LH 3 absent, 4 malformed; RF and LF 2, 3, & 4 absent, 1 & 5 and foot malformed
Yokam[d]	2001	0.10	Both hands; RH 3 absent, 2, 4, & 5 malformed; LH 3 & 4 malformed
Yuki[e]	1986	0.50	Both arms and both feet; RH and LH 1, 2, 3, & 4 and hand absent, 5 malformed; RF 3 absent, 1 & 2 malformed; LF 1 & 2 malformed

[a]Numbers in this column refer to digits, with the thumb as 1 and the little finger 5. Right is abbreviated as R, Left as L, Hand as H, and Foot as F.
[b]The focal animals included all adult females with CLMs that scored 0.1 or higher on a 0–1 index of disability developed for this project that measures the extensiveness of CLMs and accounts for specifics of limb malformation and absence, with absence weighted more heavily than malformation [Turner et al., 2008]. The index is meant to give a sense of the extent of a female's limb malformations relative to a nondisabled monkey (0) at one end of the spectrum and complete absence of arms and legs (1.0) at the other.
[c]Because of her very extensive CLMs, we included Ribbon from age 4.
[d]We added Yokam and her nondisabled control, Doro, to the study in 2007.
[e]The nondisabled control for Yuki, (Shin) died between the 2006 and 2007 field season and we replaced her with another nondisabled female (Miu), for 2007.

Later, we parsed the data into separate columns and worksheets in Excel, and then imported the data into an MS Access database. We conducted extensive error checking using a combination of manual and automatic methods in both Excel and Access. We used the statistical and graphics freeware package, R, for the analyses (R Development Core Team, 2008, http://www.R-project.org.).

We examined the data in terms of the disability status of the focal animals in two ways: we used index of disability scores [Turner et al., 2008] as a measure of the degree to which an individual was physically affected by CLMs (Table I), and we also used disability as a categorical variable, grouping all focal animals with CLMs together to compare to a group comprised of the nondisabled controls.

We controlled for other parameters that might influence the behavior of the focal animals, including dominance rank and the availability of kin. We measured the relative dominance rank among focal animals using dyadic agonistic interactions collected during focal animal follows and *ad libitum* for a total of 40 known adult females, including all focal animals. We created a social matrix using MS Excel (Version 2003), then used the program Matman (Version 1.1), to test for significant linearity of the hierarchy and the best fit for dominance rank order [Noldus Information Technology, 2003]. This sample of adult females did not include every female within the group; however, this should not affect the relative dominance rank order for known individuals or matrilines. We then gave each focal animal a rank number relative to the other focal animals for use in statistical analyses.

To compare the availability of kin, we used life history data from the Awajishima Monkey Center to establish the number of potential adult female kin available to each focal animal in each study year (H. Nobuhara and T. Nobuhara, unpublished data). We calculated the coefficient of genetic relationship using mother–daughter, sister, and grandmother–granddaughter relationships (e.g., 0.5 for mothers and daughters, 0.25 for grandmother granddaughter, and 0.25 for sisters (assuming different fathers)) [e.g., Nakamichi and Shizawa, 2003]. There was no significant difference in the average number of adult female kin available to disabled and nondisabled focal animals (Kruskal-Wallis: $X^2 = 0.2185$, df = 1, P = 0.6402). We also counted the number of living juvenile offspring (ages 1–4 years) for each focal animal for each year (H. Nobuhara and T. Nobuhara, unpublished data; S.E. Turner, unpublished data).

There was also no significant difference in the number of juvenile offspring for disabled compared to nondisabled females (Kruskal-Wallis: $X^2 = 0.5098$, df = 1, P = 0.4752).

We used linear mixed effects models (LME) for analysis, when parametric statistics were appropriate. LMEs test multiple explanatory variables, or fixed factors, within a single model and also accommodate random factors that may influence variance in the data. The influence of disability was our primary interest in these models; along with disability status, we also tested the following categories as fixed factors: the presence of an infant, the age of that infant, the presence of a 1-year-old offspring, the availability of adult female kin, the number of juvenile offspring 4 years and under, and relative dominance rank. We used the following variables as random factors in the models: individual monkey, year (which also simultaneously blocked the data by the presence or absence of a 1-year-old offspring), presence of an infant, age of the infant, and the presence or absence of heavy rain. With sufficient degrees of freedom available, the same factor can be used as both a fixed and a random factor in an LME. Using the factor as a fixed factor allows for significance testing, while keeping it in the random structure maintains the correct within-model sample sizes [Crawley, 2007].

For each behavioral variable we tested, we created a series of LMEs, the first one containing all the explanatory factors from our data which we assessed to have potential biological importance to a particular behavior. We then simplified the model by removing nonsignificant interaction terms and variables, beginning with the most complicated nonsignificant interaction term. We used the Akaike Information Criterion (AIC) to determine the model that best fit the data. When appropriate with count data and frequency scores, we used an LME with Poisson distributed errors [Crawley, 2007].

If the residuals were not Normal or Poisson distributed, or the variance was not homogenous, we tried to improve them with log+1 or square-root transformations. If transformation did not improve the data adequately, we averaged the data for a particular variable for each individual focal animal, and ran a nonparametric Kruskal–Wallis rank sum test on the means by disability category. All tests were two tailed and we considered results to be significant when P values were < 0.05.

Where we have reported or plotted mean values in the sections that follow, they represent global means weighted by individual; that is, we first averaged data (time or frequency per 30 minute focal animal follow) for each individual focal animal, then averaged these individual means to determine the average values for disabled compared to control monkeys.

RESULTS

There were no significant differences in overall time spent feeding. When we examined time spent feeding in terms of provisioned or wild food sources, there were also no significant differences. Furthermore, there were no significant differences in bite rate (tested on wild food source feeding behavior only for feeding time when visibility was good enough to count individual bites). However, disabled monkeys spent significantly less time engaged in peanuting, an activity that consists of begging for peanuts at the tourist feeding enclosure (Fig. 1A): on average disabled females spent 36 seconds per 30-minute sample compared to 78 seconds for controls (Kruskal-Wallis: $X^2 = 4.127$, df = 1, P = 0.0422). Time spent peanuting also decreased with the extensiveness of CLMs (LME: Disability Index df = 21, t-value = −2.483390, P = 0.0215). On the other hand, the two disabled monkeys with the highest disability index values (Pikaru and Ribbon) used a variant of peanuting behavior to specifically beg food from the owners of the AMC, and spent significantly more time sitting or standing at the office window, staring in intently and very occasionally receiving a high-quality food item such as a piece of fruit (Fig. 1B): Ribbon and Pikaru spent on average 105 seconds per 30-minute sample "window sitting" compared to 2 seconds for all other focal animals (Kruskal-Wallis: $X^2 = 6.1139$, df = 1, P = 0.01341).

Total time spent engaged in locomotion was not different among disabled and nondisabled females, although mothers with infants spent less time traveling than other females (LME: df = 28, t-value = −3.035428, P = 0.0051). There were no significant differences in speed of locomotion for disabled and nondisabled monkeys, in terms of time spent engaged in "walking" versus "running" behaviors. There was also no significant time difference in total time spent arboreally, nor in the time focal animals spent using the low (<10 m) or high (>10 m) canopy.

Style of locomotion can be affected by CLMs: many individuals with CLMs have an uneven gait, or less subtly, use habitual bipedalism. There were two monkeys in our focal sample who employed habitual bipedalism (Fig. 2), a difference that is clearly evident when watching these monkeys move around. We quantified this significant difference by testing mean time spent in bipedal locomotion for these two monkeys compared to all other focal animals. While all monkeys spent a similar amount of time moving, Yuki and Ribbon spent 104 seconds per 30 minute follow engaged in bipedal locomotion, compared to 0.45 seconds on average for all other focal animals (Kruskal-Wallis: $X^2 = 5.8902$, df = 1, P = 0.01522).

Grooming style was also different according to disability (Fig. 3). Disabled adult females had a significantly lower rate of hand use for removing louse eggs while grooming others: a rate of
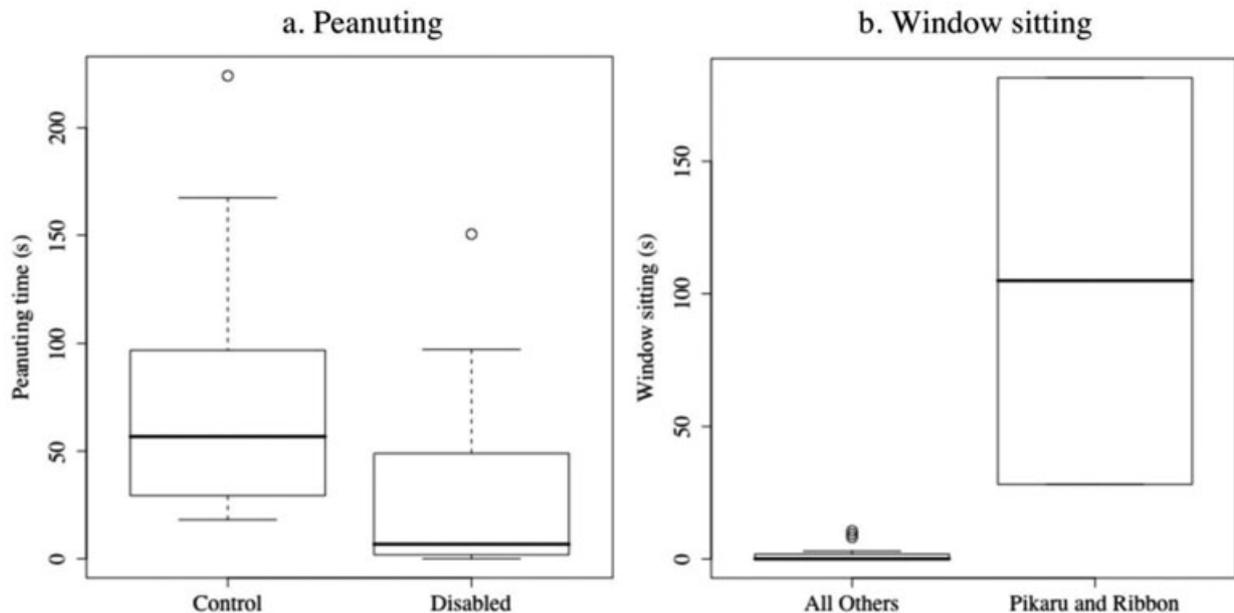
Fig. 1. (A) Boxplot of average time per 30-minute focal follow spent engaged in "peanuting" by disabled females and controls. In the boxplot, the thicker horizontal line inside the box shows the median value. The top and bottom of the box show the first and third quartiles (the 25th and 75th percentiles). The difference between the top and bottom lines is the interquartile range. If there are no outliners, then the dashed vertical lines show the maximum and minimum values for the data. If there are outliners, 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]. (B) Boxplot of average time per 30-minute focal follow that Pikaru and Ribbon engaged in "window sitting" compared to all other focal animals. These two focal animals with extensive CLMs engaged in a variant of "peanuting" behavior, spending significantly more time sitting at the office window, staring in intently, and occasionally receiving a high-quality food item from the owners of the AMC.

0.08 skin-to-hand-to-mouth actions per minute compared to 0.18 for controls (Kruskal-Wallis: X^2 = 7.6705, df = 1, P = 0.005613). Instead, they used two distinctive louse-egg removal grooming techniques significantly more than nondisabled controls: direct use of the mouth (Fig. 3E) and a two-arm pinch on the hair (Fig. 3F). Disabled females had a mouth-to-skin rate of 0.15 times per minute while grooming compared to 0.02 times per minute for nondisabled controls. Two-hand/arm pinching was relatively rare and only used by disabled females who lacked functional opposability in both hands (mouth: Kruskal-Wallis: X^2 = 11.0455, df = 1, P = 0.000889; two-arm pinch: Kruskal-Wallis: X^2 = 4.2903, df = 1, P = 0.03833).

Disabled monkeys engaged in a higher frequency of self-scratching behavior (Fig. 4) (LME with Poisson for disability index: Z = 2.06, P = 0.0394). This difference occurred primarily because of significantly more scratching with the foot (as opposed to the hand) with disabled females scratching with the foot 3.3 times per 30-minute sample compared to 2.3 times for nondisabled controls (LME with Poisson errors for disability index: Z = 2.614, P = 0.00895). Disabled monkeys also had another significant difference in the method of self-scratching. Monkeys with extensive CLMs sometimes scratched their bodies against substrates, such as structures at the AMC, roots, or rocks. This method of self-scratching was

used relatively rarely and was nearly exclusive to disabled animals, particularly Ribbon, and increased in frequency according to the extensiveness of CLMs (LME with Poisson distribution for disability index: Z = 3.061, P = 0.00220).

In addition to these quantified differences, there were a number of other disability associated behavioral differences that we observed at AMC. Some of these behaviors included innovative solutions to individual problems, some were modifications of existing behaviors to suit the needs of a disabled individual. Innovative behaviors and behaviors that were observed frequently for disabled animals but infrequently for controls are summarized in Table II.

DISCUSSION

How do CLMs Influence the Behavior of Adult Female Japanese Macaques, Particularly in Relation to Feeding and Locomotion?

In many ways, there was a striking similarity in the behavior of adult females with CLMs and those without CLMs. Females with CLMs were engaged in the same types of daily behaviors as nondisabled females. They lived within the social group and there were no behaviors on our ethogram that were only used by nondisabled females. A casual observer would find little to distinguish the overall behavior
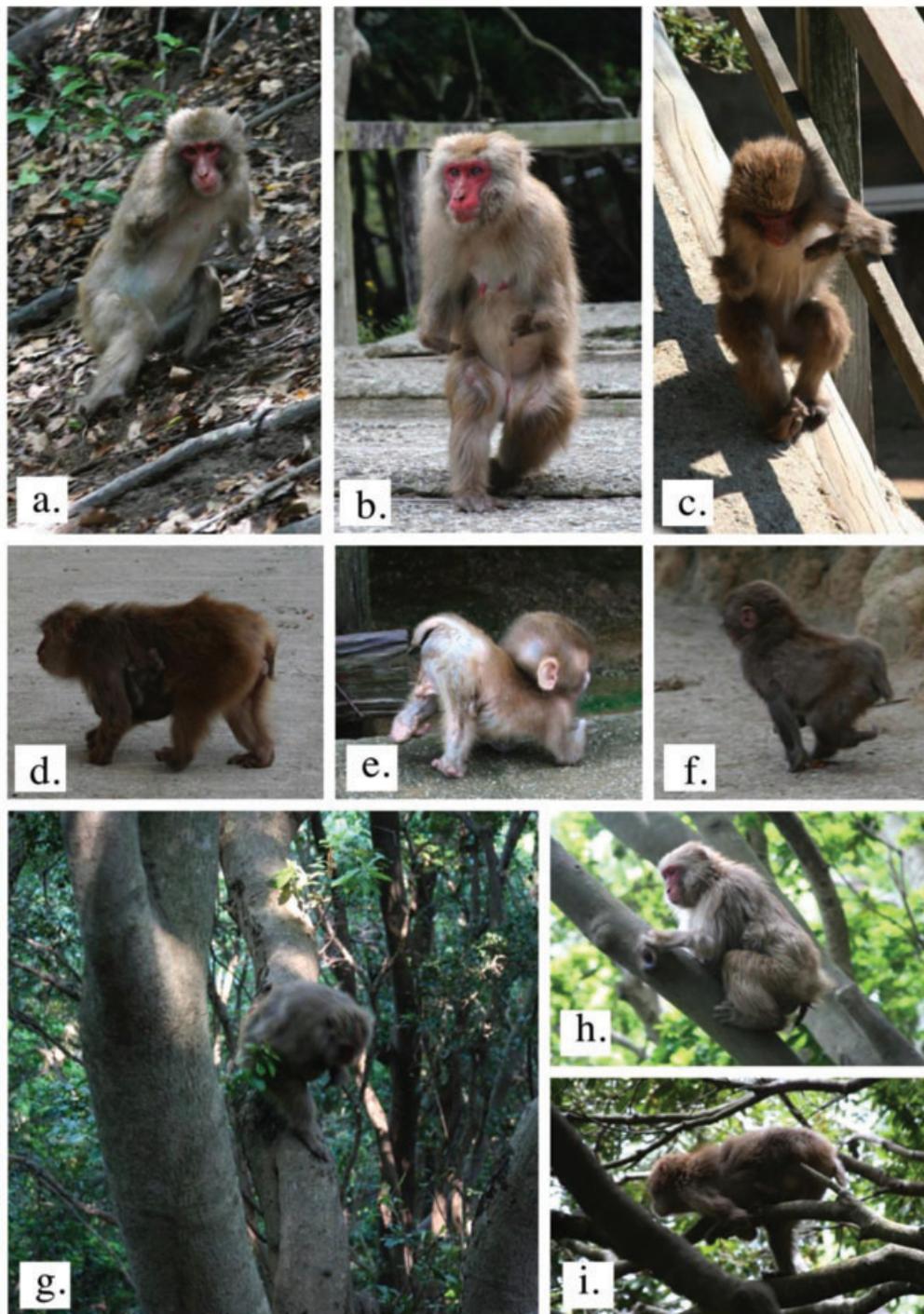
Fig. 2. Examples of locomotion among disabled Japanese monkeys: (A) Ribbon employing her sideways hop-run bipedal locomotor style; (B) Yuki walking bipedally; (C) Ribbon using the railing while walking bipedally down a ramp at AMC; (D) Pikaru, an adult female focal with extensive CLMs on all four limbs, who does not employ habitual bipedalism, and appears to be at a locomotor disadvantage; (E) Sunday07, an infant with extensive CLMs on all four limbs and limb length inequality, beginning to develop independent locomotion; (F) Biwa, a 1-year-old juvenile with extensive CLMs on all four limbs and limb length inequality, running with weight-bearing emphasis on his left forelimb and right hind limb; (G) Yuki climbing down the trunk of a tree in a bipedal position; (H) Punch climbing a smooth trunk; (I) Ribbon climbing to the terminal branches in the high canopy to feed on *M. rubra* fruit. Versions of panels A and C also appear in Ribbon's Way, by Sarah E. Turner (Sono Nis Press, Winlaw, BC, Canada).
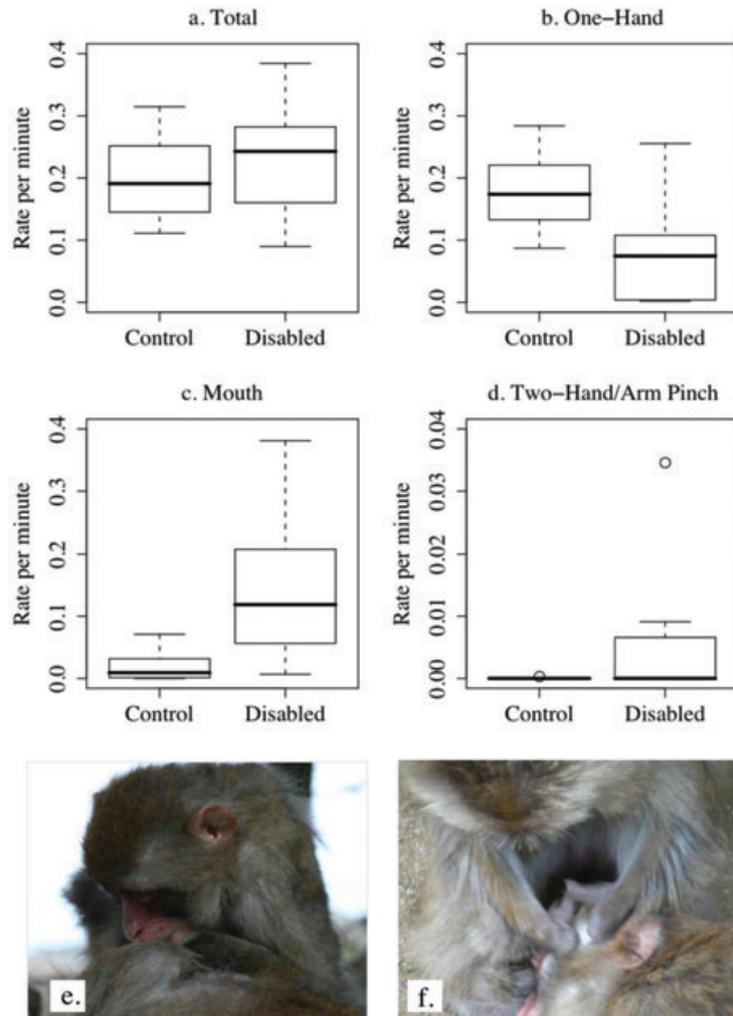
Fig. 3. Boxplots of mean rates of grooming method use per minute of grooming time (in which visibility was adequate to count hand-to-mouth and mouth-to-body motions); (A) total rate of all methods used; (B) rate of one-handed pick-up of louse egg or debris to bring it to the mouth; (C) rate of direct 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. For a description of the boxplot, see Figure 1. Examples of grooming styles used by disabled monkeys: (E) direct mouth use; (F) two-arm (or two-hand) pinch to remove a louse egg from the grooming recipient's hair. Versions of panel E also appear in Ribbon's Way, by Sarah E. Turner (Sono Nis Press, Winlaw, BC, Canada).

of disabled and nondisabled females at AMC. Particularly in terms of feeding and locomotion, our data suggest that CLMs have little influence on many aspects of these behaviors.

In relation to feeding, we had hypothesized that (i) disabled females would rely more on provisioned foods than nondisabled females, spending more time provision feeding than nondisabled females and that (ii) disabled females would not feed as efficiently as nondisabled females, however, neither hypothesis was supported by the data. Disabled adult females did not appear to rely more heavily on provisioned foods than did nondisabled controls; time spent eating provisioned foods and wild foods were similar for all focal animals. We wondered whether a lack of difference in time spent feeding might mask a difference in the amount of food ingested if disabled

monkeys were less efficient feeders than nondisabled monkeys, however, this hypothesis was not supported by the data. The lack of a significant difference in bite rate when feeding on wild food sources suggests that monkeys with CLMs are in general able to maintain similar levels of feeding efficiency compared to controls. These results mirror those of Stokes and Byrne [Stokes, 1999; Stokes and Byrne, 2001] who found that for complex food processing techniques, all but the most extensively disabled chimpanzees fell within the normal range of feeding efficiency. Similarly, Kano [1984] reported that dominance rank, more than disability, accounted for access to food in wild bonobos.

We had expected that disabled monkeys would rely more on provisioned foods to help compensate for CLMs, either in response to reduced feeding
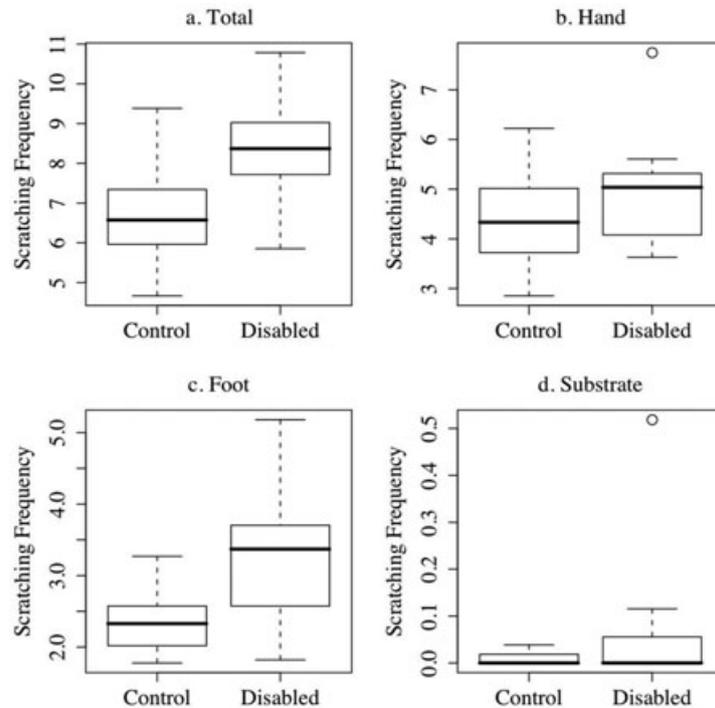
Fig. 4. Boxplots of average frequency of self-scratching per 30-minute focal animal follow; (A) total frequency; (B) frequency of selfscratching using the hand to scratch; (C) frequency of self-scratching using the foot to scratch; (D) frequency of self-scratching in which the focal animal used a substrate in the environment on which to scratch their body. Note that the y-axis scales in these plots are not the same. For a description of the boxplot see Figure 1.

efficiency, higher energy requirements due to reduced locomotor efficiency, or both. It was initially surprising to find little influence of disability on time spent feeding on provisioned food. However, access to supplemental human-sourced foods, either through provisioning or crop raiding, is known to reduce the modification of activity budget under other circumstances [Saj et al., 1999; Van Doorn et al., 2010], such that individuals who would likely need to modify activity budgets were able to avoid doing so because of the availability of high-quality human-sourced foods. For example, Saj and colleagues [1999] found that lactating vervet monkeys with access to human sources of food were able to maintain their activity budgets without making changes in foraging time to meet energy needs. In the food-rich environment at Awajishima, monkeys with CLMs seem to be generally able to compensate for disability without having to spend more time feeding. Also, as Millette and colleagues [2009] pointed out, living within a social group can constrain the ability of individuals to modify activity budgets, in that travel time may be fairly inflexible if individuals wish to remain with the group. For the monkeys at AMC, time spent feeding on provisioned foods is also constrained by group movement and food availability, so spending much more time feeding on provisioned foods may not have been possible and sifting through the dust and leaves for a few extra grains may not have been energetically worthwhile. For wild chacma baboons, in circumstances where infanticide threat likely constrained feeding time because of increased vigilance requirements (vigilance was substantially higher during rest time), lactating females were found to partially compensate for energetic challenges by increasing rest time [Barrett et al., 2006]. For the disabled monkeys at Awajishima, travel and feeding time may also be somewhat constrained, and increased rest time may help compensate for disability associated with CLMs (S.E. Turner and colleagues, unpublished data).

By one measure, disabled monkeys are actually less reliant on provisioned foods than their nondisabled counterparts. Disabled monkeys spent significantly less time begging for peanuts at the tourist enclosure. We suspect that this behavioral difference reflected the difficulty of grasping peanuts through wire fencing, and perhaps a tendency among tourists to avoid giving peanuts to monkeys with CLMs, possibly because of inhibition around placing peanuts directly into the mouth of a monkey through the fence. Two of the most disabled females, Ribbon and Pikaru, did gain access to some high-quality provisioned foods by sitting at the office window begging from the owners of the Monkey Center, a fairly successful method of obtaining extra food for these monkeys.

TABLE II. Disability associated behaviors at AMC

Behavior	Description	Comments
Styles of locomotion and locomotor variants (Fig. 2)	• Habitual bipedal locomotion	• Used habitually by some disabled monkeys with limb configurations that permit it and who develop its use

	• Walking or running on the hind legs
	Some individual variations include:
	  • 2-legged hop: forward bipedal hopping motion with both legs together
	  • Sideways bipedal hop-run: rapid sideways-facing forward hopping movement
	    • Bipedal climbing: use of bipedal locomotion on more horizontally oriented tree branches
		• Individual variations observed at different stages of development and among various disabled individuals

	• Unusual styles of quadrupedal locomotion	• Individual variations observed at different stages of development and among different disabled individuals

	• Disabled monkeys employ a variety of styles of quadrupedal locomotion that reflect a combination of their individual limb configurations and the individual's associated behavioral modifications. Styles of quadrupedal locomotion often involve an uneven gait, and emphasis on particular limbs for weight-bearing.
	Some individual variations include:
	  • Grasshopper-style hop: use of back legs to propel the body forward onto all fours
	    • Favoring a tri-pedal walk
	    • Favoring the hind legs in a quadrupedal position
	    • Running using primarily one forelimb and one hind limb from opposite sides of the body	

• Use of two-arm pinch for climbing	• Elbows or forearms pinch the trunk of the tree and hind legs are used as leverage with a hopping motion	
• Use of elbow for climbing	• Some monkeys with extensive manual disabilities hook their elbow over a branch during climbing	
• Use of banister as support	• Regular resting of the arm on the ramp rail, while walking bipedally on a ramp at the AMC	• Used regularly by one disabled monkey (Ribbon)
• Use of banister as slide	• Sliding down a wooden banister on ventrum as a regular means of getting down a ramp at AMC	• Used by at least two extensively disabled juveniles

TABLE II. Continued

	Behavior	Description	Comments
Infant carrying positions	• Bipedal support hip carry	• Mother holds the infant on her hip by squeezing with one arm, during bipedal locomotion	• Innovative position observed with one disabled mother (Yuki) for multiple offspring
	• Bipedal support ventral carry	• Mother holds the infant on her front with one or both arms during bipedal locomotion	• Used primarily by habitually bipedal mothers (Yuki during this study and later Ribbon)
	• Bipedal dorsal carry	• Infant clings to the mother's back during bipedal locomotion	• used primarily by habitually bipedal mothers (Yuki during this study and later Ribbon)
Feeding and Foraging	• Use of feet for foraging for invertebrates	• While foraging for invertebrates in the leave litter, monkeys usually use their hands to disturb the leaf litter and then catch invertebrates between thumb and forefinger for consumption. One extensively disabled female was observed employing a different technique on several occasions, in which she sat on the ground with her legs straight out in front of her body, pounded the ground with her legs, sometimes moving them side to side, then caught the invertebrates directly with her mouth.	• Innovative technique used by one extensively disabled female (Ribbon)
	• Processing of green *Mgrica rubra* and withered *M. rubra*	• The usual process for nondisabled monkeys eating green *M. rubra* fruit is to pick a fruit using thumb and forefinger and place it in the mouth, or pick the fruit directly from the cluster with the mouth, then crack the seed in their jaws, and extract the shell debris from the mouth manually. Monkeys with extensive manual disabilities or absence of hands picked the green fruit directly from a cluster with their mouths, then cracked the seed in their jaws. They then spit the seed and shell pieces onto the surface of their hand or arm, and removed the seed with their mouths, discarding the shell debris.	• Modification of existing behavior pattern that usually involves precise manual manipulations
	• processing of withered *M. rubra*	• For withered, old *M. rubra* fruit, nondisabled monkeys rubbed the fruit vigorously between the palms of their hands then brought it to the mouth manually, cracked the shell and removed the debris manually; disabled monkeys followed the same pattern they used for green fruits.	• Modification of existing behavior pattern that usually involves precise manual manipulations
	• Two-hand/arm pinch during provision feeding	• Nondisabled monkeys usually pick up individual small provisioned food items (grains or soy beans) between thumb and forefinger; some disabled monkeys used a precise pinch between distil ends of arms or between two hands to move food items to the mouth.	• Disability specific, only used by some monkeys who lack the use of both hands

TABLE II. Continued

Behavior	Description	Comments
• Aggregating provisioned grains	• Pushes small provisioned food items (grains and soy beans) into a pile and eats directly off the ground	• Used by some manually disabled monkeys
• Two-hand grain conveyance	• Pushes small provisioned food item with one hand onto the other, then brings the food item to the mouth	• Observed in one disabled female (Pikaru)
Grooming and Scratching (Figs. 3 and 4)		
• Mouth use during grooming	• Direct use of the mouth for removingxst louse eggs and debris while grooming	• Used occasionally by many monkeys, but significantly more by disabled monkeys
• Elbow push in grooming	• Use of the elbow to push hair out of the way and hold it down during grooming	• Observed in one disabled female (Ribbon)
• Two-hand/arm pinch in grooming	• Hands or the ends of arms are brought together to make a pinch to remove louse eggs and debris when grooming	• Disability-specific, monkeys without pinching ability in either hand
• Self-scratch on substrate	• Scratching of the body against a protrusion or rough surface in the environment	• Almost entirely disability specific
Other		
• Examine water with feet	• Monkeys at AMC often "examine water", sit and manipulate the surface of the water with a hand, splashing and making bubbles, while staring intently at their activity. An individual without hands created similar drips, bubbles, and splashes with her feet.	• Many monkeys perform the same motions with hands; feet used for this behavior by one individual (Ribbon)

In terms of locomotion, we had hypothesized that (iii) disabled females would locomote more slowly than nondisabled females, spending less time running, and more time walking, and that (iv) disabled females would spend less time in the canopy overall, and especially less time in the high canopy (>10 m). However, neither hypothesis was supported by the data. In this study, we used a relatively simplistic measure for speed of locomotion, grouping all walking-related behaviors together and all running-related behaviors together and examining the time spent engaged in each speed category. At this level of analysis, there were no differences between disabled and nondisabled monkeys. However, while this provided a picture of what the monkeys were doing on a day-to-day basis, it did not illuminate what they were potentially capable of doing if the need were to arise—for example to escape predation by a feral dog or avoid being hit by a car on the road. There were disabled monkeys who appeared to move more slowly than other monkeys, and appeared to be unable to run or move very rapidly. Some *ad libitum* observations provide qualitative information about capability. For example, in one instance of juvenile play, we watched three young monkeys running, at what appeared to be full speed across a flat, approximately 5 m wide concrete surface. The two nondisabled juveniles reached the other side of the deck in tandem, while the young male with extensive CLMs on all four limbs was only half way across the space at the same time. In a different study conducted at AMC on mothers and infants and disability, one disabled female with extensive malformations on all four limbs was never observed running during 4 months of data collection [Turner, 2003]. Also, when feral dog barking is heard, the monkeys at AMC would run from the provision feeding area for the forest, with apparently a similar motivation to run, and it appeared as though some extensively disabled females were slower in this circumstance than their nondisabled counterparts. It appears that the monkeys who experience the most negative affects of CLMs in terms of locomotor ability are those with extensive CLMs on three or four limbs, in an asymmetrical configuration such that balance and gait are affected, and who do not employ habitual bipedalism in their locomotion.

Also, although in general, disabled monkeys were able to climb trees very well, for the most extensively affected individuals, we think there were some climbing circumstances that they were not capable of negotiating. In particular, trees with very smooth and vertical trunks probably pose difficulty for some disabled females, however such a lack of ability is difficult to document, as they likely compensated by selecting suitable climbing trees. A particular instance with a juvenile male illustrated what was likely a general difficulty for many individuals with extensive CLMs: on one very rainy day, we observed a juvenile male who was looking up at his mother, calling and repeatedly hurling himself in her direction. She was sitting on a structure about 1.5 meters above him at the top of a vertical post. He was clearly motivated to get to her location, but whenever he tried to climb the post, he slipped down again. Nondisabled monkeys climb this same structure without any apparent difficulty. Finally, the juvenile found an alternative climbing pathway, leaping over to a nearby bush and climbing up and around to reunite with his mother. This example is informative on a couple of levels: it showed a limit to a disabled monkey's physical abilities, but also his ability to devise a new way to achieve his goal.

It is likely that despite behavioral compensations, monkeys with extensive CLMs experience increased risk of injury and mortality associated with climbing and predation. We have seen disabled monkeys slip in the trees a number of times. However, there is little evidence that this potential for increased risk curtails their climbing behavior; disabled monkeys can be found in the highest branches, climbing steep cliffs of crumbling clay, balancing on precarious ledges, and even leaping across gaps between buildings at the Monkey Center.

How do Adult Female Japanese Macaques with CLMs Compensate for Physical Impairments?

While there were few differences associated with the overall types of behaviors found among adult females at AMC, we did observe differences in behavior associated with disability, in terms of those behaviors used to compensate for CLMs. Some compensatory behaviors were subtle (e.g., the probable selection of climbable trees), others were somewhat more obvious (e.g., the use of two-hand/two-arm pinch during grooming, discussed below), and some were very obvious to even a casual observer (e.g., use of habitual bipedalism by some disabled monkeys).

We expected and were able to quantify habitual bipedalism in some focal animals. There were two focal animals that were habitually bipedal. In addition, we observed many, more subtle, variations on the even-gait quadrupedal norm. The style of locomotion used by a disabled adult Japanese macaque reflects a combination of their individual limb configurations and the individual's behavioral modifications and development. When a disabled infant is born, it is possible to guess as to the style of their adult locomotion, but even experienced observers cannot say with certainty if an infant will be bipedal, quadrupedal, or tripedal or what individual variations of these forms of locomotion the adult monkey will employ. This is an example of the behavioral flexibility of individual Japanese macaques, and the nexus in disability between an individual's unique physical circumstances and how these translate into behavior for that particular individual within their environment.

We predicted that disabled females would modify behaviors that usually require four limbs and/or precise hand use. We hypothesized that (v) disabled females would use different grooming techniques compared to nondisabled females, in particular, we expected to see more use of the mouth and unusual patterns of hand usage. Grooming behavior for most monkeys employs considerable digital dexterity to comb hair through fingers, and loosen, pinch and grab ectoparasites and debris, and nondisabled monkeys employ a variety of techniques when they groom [Tanaka, 1995]. Monkeys with manual physical impairments would by necessity need to modify techniques or employ different techniques in order to participate in social grooming. In this study, we found that disabled monkeys used the mouth directly in the removal of louse eggs significantly more than other monkeys, and that some of the females also used a two-arm pinch to comb out and remove louse eggs from the hair. Furthermore, Ribbon used her elbows for parting the hair to find louse eggs. Although it is likely that these alternate, disability associated techniques are not as efficient at louse egg removal as those of nondisabled monkeys, manually disabled monkeys are able to remove louse eggs using these alternate techniques. Perhaps more importantly, however, these techniques facilitated grooming that appears to be socially effective.

We hypothesized that (vi) disabled females would use different techniques associated with self-scratching, a hypothesis that was supported by the data, which showed significantly more use of the foot for self-scratching, as well as disability-associated scratching against substrates. We also hypothesized that (vii) disabled females would use different feeding techniques than nondisabled females, and we did observe qualitative differences in the way that disabled females fed on provisioned foods as well as some wild foods, such as when they fed on green or withered *Myrica rubra* fruit (Table II). We also expected to see other disability associated behaviors, including the innovation of novel solutions to individual disability challenges. As is outlined in Table II, there are also many stylistic ways that disabled monkeys, particularly the most extensively disabled monkeys, such as Ribbon and Yuki, behaved differently from those around them. These differences, some of them behavioral innovations, were not always quantified or readily quantifiable, but are nevertheless important. Kummer and Goodall [1985] discussed the conditions for innovative behavior in primates. They noted that innovations are more likely to occur at times when food is plentiful, which gives individuals the ability to use more time for non-essential activities, and in circumstances such as illness or disability where an individual must figure out a way to function and compensate [Kummer and Goodall, 1985]. At AMC, therefore, disability and provisioned feeding create circumstances favorable to observing behavioral flexibility and innovation. Stokes and Byrne [2001] found that for manually disabled chimpanzees, compensatory behavior in relation to food processing involved modifying existing techniques, employing novel steps in techniques that already existed in the behavioral repertoire of the group. Similarly, many of the compensatory behaviors we observed at AMC were behaviors present in the repertoire of the group as a whole, but were used differently in terms of time or frequency or were modified slightly by disabled animals (e.g., bipedal locomotion, supported carrying and nursing of infants, and mouth use in grooming). However, we also observed some novel disability-specific behaviors (e.g., Yuki's bi-pedal hip-carry, and the two hand/arm pinch in grooming). Ribbon's method for foraging for insects among the leaves is particularly noteworthy as an innovation (Table II). She may very well have stumbled across her method by chance, but even so, she behaved as though she was able to recognize the utility of the technique and employed it on numerous occasions.

Japanese macaques are well-known for their innovative abilities: early studies on *M. fuscata* at Koshima Island were some of the first to document such abilities, with the young female "Imo", who began washing sweet potatoes in the ocean [Kawai, 1965]. In the decades that have followed, there have been many other documented examples of behaviors innovated and spread across the social group, and becoming social traditions in many nonhuman primates populations and species [Bonnie and de Waal, 2006; Fragaszy and Perry, 2003; Huffman and Hirata, 2003; van Schaik et al., 2006], including stone handling in Japanese macaques [Huffman and Hirata, 2003; Huffman and Quiatt, 1986; Leca et al., 2008].

What are the Adaptive Implications of Disability Associated Behavioral Flexibility and Innovation?

The relative similarity of behaviors between disabled and nondisabled animals has interesting implications for our understanding of behavioral flexibility and disability-associated behaviors in nonhuman primates. While many of the adult females in this study had extensive limb malformations (Fig. 2 and Table I), and while the form of locomotion, grooming, and self-scratching behaviors was different for disabled females, the time spent engaged in life-sustaining behaviors such as most feeding behaviors and locomotion was not, suggesting that females who survive to adulthood with CLMs were able to compensate for physical impairments by individually modifying their style or techniques, without losing overall functionality for many types of behavior. They developed adequate individual styles of

locomotion, including habitual bipedalism, such that CLMs appeared to have little influence on overall climbing, travel, and foraging ability in adult females. Similar compensatory ability has also been observed in great apes [Kano, 1984; Stokes, 1999; Stokes and Byrne, 2001] and *L. catta* [Cuozzo and Sauther, 2004; Millette et al., 2009].

The disabled monkeys at AMC provide examples of how behavioral flexibility and innovation can potentially contribute to offsetting costs of physical impairment, such as increased mortality risk and reduced reproductive success [Carey et al., 2007]. The ability to behave flexibly and innovate in adverse circumstances such as those experienced by disabled individuals would facilitate survival and reproduction for individuals who would otherwise experience reduced fitness. Although it is likely that not all individuals with CLMs, particularly those with the most extensive CLMs, would survive in a wild context, these individuals illustrate how animals who are otherwise at a disadvantage can improve their chances of survival and reproduction through compensatory behavior and innovation.

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