Chapter 8

Disability and Dominance Rank in Adult Female and Male Japanese Macaques (*Macaca fuscata*)

Sarah E. Turner, Masayuki Nakamichi, Toshikazu Nobuhara, Hisami Nobuhara, and Simon M. Reader

Abstract More than 30 years ago, Fedigan (Primate paradigms: sex roles and social bonds, 2nd, 1992 edn. Eden Press, Montreal, 1982) recognized and emphasized that social dominance was not just a reflection of physical size, strength and aggression in nonhuman primates but rather involved a multitude of complex factors and social dynamics. In the free-ranging group of Japanese macaques (*Macaca fuscata*) on Awaji Island, Japan, physical disabilities in the form of congenital limb malformations (CLMs) affect around 17% of the population. This group provides an opportunity to examine dominance rank in relation to physical impairment. Here, we present an analysis of dominance rank in the adult female and adult male Japanese macaques in the Awajishima group using behavioural data collected in 2005, 2006 and 2007 on 38 adult females (12 with CLMs) and in 2015 on 22 adult males (7 with CLMs). Once we controlled for matrilineal kinship, we found that disabled females tended to hold somewhat lower than expected dominance ranks. In contrast, disabled males were interspersed throughout the rank order, and disability was not associated significantly with dominance rank. However, age class had a statistically significant effect on dominance rank in males, such that older males tended to rank higher than younger males. Our results underscore Fedigan's insights by demonstrating some of the complexities of dominance relationships in the context of the extensive physical variation shown in this group of Japanese macaques.

Keywords Dominance rank · Physical impairment · Resource holding potential · Japanese monkey · Physical disability

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S. E. Turner (✉) · S. M. Reader
Department of Biology, McGill University, Montreal, QC, Canada
e-mail: sarah.turner@concordia.ca

M. Nakamichi
Osaka University, Osaka, Japan

T. Nobuhara · H. Nobuhara
Awajishima Monkey Center, Hyogo Prefecture, Japan

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8.1 Introduction

Dominance is often used to describe the relationship outcome of the pattern of agonistic interactions between pairs of individuals (Drews 1993). When dyadic agonistic encounters between individuals consistently result in one individual taking physical precedence, obtaining a sought-after food item or otherwise "winning" a contest, fight or interaction, this individual is described as being dominant over the other, subordinate, individual (Drews 1993). In a diverse array of animal species, it is possible to rank individuals in a linear fashion according to their dominance relationships (Shizuka and McDonald 2015). Dominance rank is an emergent property of patterns in social interactions, and as such it should not be taken as a proxy for other variables, such as higher fitness, without clear evidence to suggest a direct connection (Fedigan 1982). However in a wide variety of species, an individual's dominance rank has been shown to influence fitness-associated processes and outcomes, such as access to food and mates, growth patterns, parental care and investment, as well as health measures such as stress hormones and parasite transmission (Abbott et al. 2003; Berard 1999; Dey et al. 2015; Drews 1993; Jack and Fedigan 2006; Majolo et al. 2012; Manson 1992; Sapolsky 2005). A recent meta-analysis of dominance rank and fitness in primates suggested that there are often fitness benefits associated with high dominance rank (Majolo et al. 2012). In particular, higher dominance rank was associated with having a higher proportion of infants surviving their first year of life for females and higher fecundity and mating success in males (Majolo et al. 2012). However, there is considerable inter- and intraspecific variation across primates; there can be costs (such as stress, e.g. Abbott et al. 2003; Sapolsky 2005) and benefits (such as increased mating and paternity success, e.g. Alberts et al. 2006, 2002) to high and low dominance rank that depend on many behavioural, physiological and ecological factors (Abbott et al. 2003; Majolo et al. 2012).

Dominance has been studied extensively in many animal species (Drews 1993; McDonald and Shizuka 2013; Shizuka and McDonald 2015) and has been of particular interest in the study of nonhuman primates (Bergstrom and Fedigan 2010; Drews 1993; Fedigan 1982; Majolo et al. 2012; McDonald and Shizuka 2013; Nakamichi et al. 1995a). More than 30 years ago, Linda Fedigan (1982) provided an in-depth critique and analysis of studies on dominance rank in nonhuman primates. She pointed out that studies of dominance had focused on how animals "organize themselves according to the ability to physically defeat, or intimidate others in conflict" (p. 93), while they often overlooked the many other life history and behavioural factors associated with animal social organization. Fedigan (1982) pointed out that many studies emphasized males and the role of strength and fighting ability in shaping dominance interactions. She argued that the determinants of dominance are complicated, context dependent, only part of an animal's social organization and that "studies of primates generally show that dominance is not… determined primarily by the physical attributes of size and strength" (Fedigan 1982, p. 101).

There are numerous definitions of dominance in the scientific literature; however, dominance is most often measured using contests between individuals (or models of contests between individuals) (Kokko 2013). Individuals vary in terms of their resource holding potential (RHP) (or resource holding power), which is often defined as an individual's ability to win a dyadic all-out physical fight if such a fight were to occur (Kokko 2013; Parker 1974). Fighting ability has been described as "the primary determinant of rank in primates", at least for males, although the authors also wrote that "there is certainly sexual selection on traits other than fighting ability, and there are other sources of variance in male mating and paternity success" (Alberts et al. 2006, p. 1177).

Physical impairment would be expected to have a negative influence on RHP, such that we might expect that the more extensive an individual's physical disabilities, the lower their RHP and the lower their position in the dominance rank order. However, an individual's actual ability to hold resources may not always reflect, or not strongly reflect, their ability to win in a dyadic all-out fight. There are many examples reported of individuals who are very old, injured, toothless or physically disabled living within primate groups and holding high dominance rank positions, as well as individuals employing apparently intelligent strategies to improve their rank or circumvent dominant individuals (Cuozzo and Sauther 2004; Fedigan 1982; Kummer and Goodall 1985; Millette et al. 2009; Nakamichi et al. 1995b; Reader and Laland 2001; Schaller 1963; Stokes and Byrne 2001).

Since the 1960s, ~17% of infant Japanese macaques (*Macaca fuscata*) in the free-ranging group of at the Awajishima Monkey Center on Awaji Island, Japan, have been born with malformations of the limbs and digits (Nakamichi et al. 1997; Turner et al. 2008; Yoshihiro et al. 1979). Many of these disabled individuals survive to adulthood, so that within the group at Awajishima, there are numerous adult females and males with physical impairments. The extent of individual congenital limb malformations (CLMs) varies considerably, ranging from relatively mild malformations of digits or absence of a finger or two to combinations of extensive malformation and absence affecting the hands, feet and limbs or portions thereof (Fig. 8.1). Research has shown that adult females, at least, are able to compensate behaviourally for CLMs; in most respects their behaviour does not differ from that of nondisabled females; however, they perform certain behaviours in unique ways such as using a two-handed/two-arm pinch for grooming and employing individually appropriate styles of locomotion and infant carrying (Turner et al. 2012). Mothers of disabled infants tend to provide compensatory care as well, using an arm to support an infant who is unable to cling to its mother during locomotion and nursing (Turner et al. 2005); otherwise, however, there is little evidence for conspecific care associated with disability in the group (Nakamichi et al. 1983; Turner et al. 2014). However there is also little evidence to suggest social selection against disabled monkeys in the Awajishima group, and disability generally elicits an undifferentiated social response from conspecifics (Turner et al. 2014).

Japanese macaques are known for their formation of stable linear dominance hierarchies, with higher-ranking individuals often having priority of access to contestable food resources and also tending to receive more and give less grooming

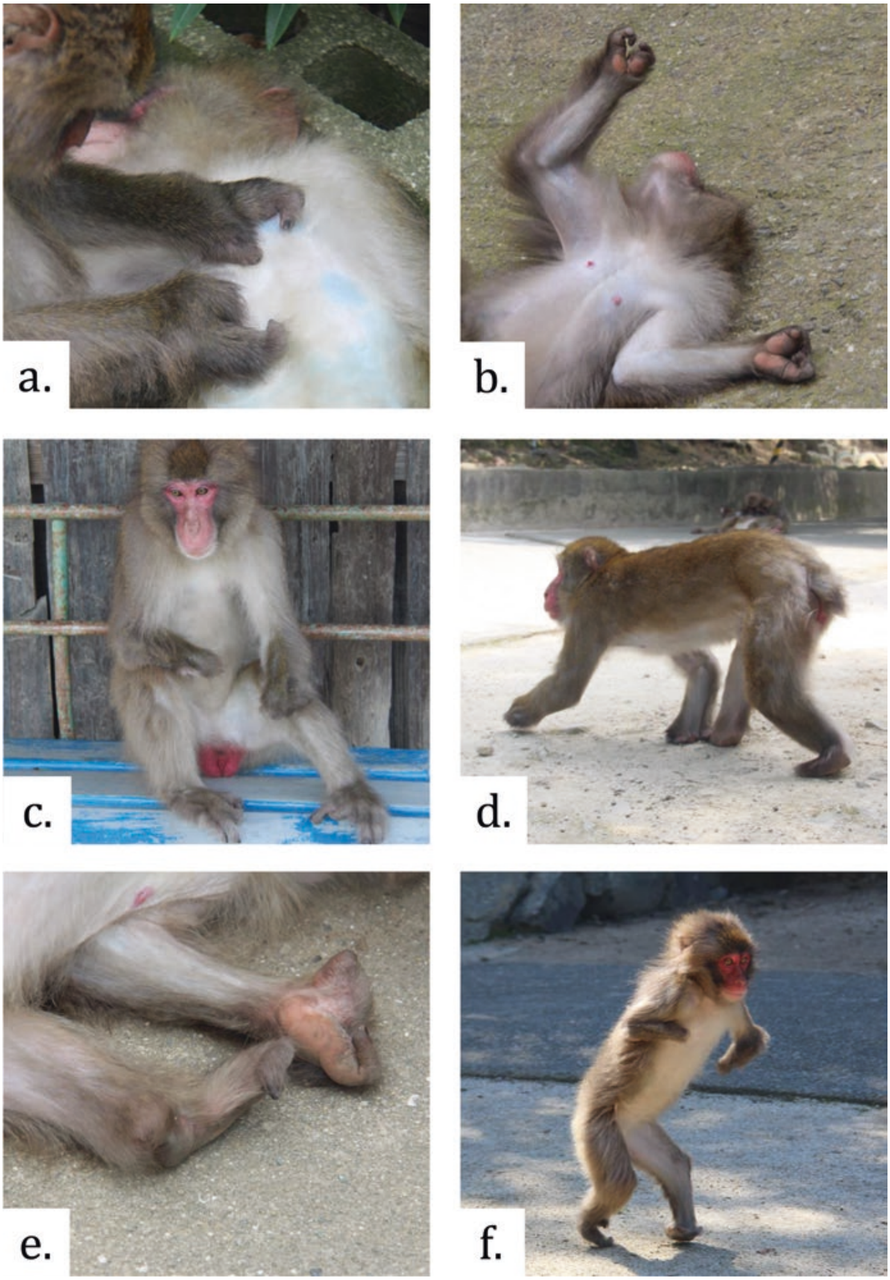

Fig. 8.1 Examples of individuals with congenital limb malformations at Awajishima. (**a**) and (**b**) show top and bottom views of the hands of two young males with similar hands: (**a**) Mochi (born ~2005, index of disability 0.35) and (**b**) Chonan (born 2001, index of disability 0.28). Their hands both show the absence of digits 2, 3 and 4 as well as associated metacarpal bones; (**c**) Gatsu, (born 2005, index of disability 0.47) a young male with the absence of hands and malformations on his

than lower-ranking individuals (Nakamichi et al. 1995a; Nakamichi and Shizawa 2003). Japanese macaques are female philopatric, and kinship is known to be a strong predictor of female dominance rank. In his 1958 study of the provisioned Minoo group of Japanese macaques, Kawamura (1958) discovered two patterns related to female kinship and dominance rank. He observed that (1) mothers outranked their daughters and (2) younger sisters outranked their older sisters. From these observations, he proposed two rules to predict dominance relationships in female Japanese macaques: that females acquire a dominance rank just below that of their mother and the idea of youngest ascendancy (that sisters hold dominance rank inversely ordered by age). These two patterns are now often called "Kawamura's rules" and have been found to be a strong and consistent predictor of female dominance relationships in Japanese macaques (especially in provisioned groups), as well as in other primate species (Bergstrom and Fedigan 2010, 2013; Fedigan 1982; Koyama 1967, 1970; Nakamichi et al. 1995a; Nakamichi and Yamada 2010). Kinship has such a strong influence on dominance rank in female Japanese macaques that other factors such as age and physical characteristics generally have less influence on rank (Nakamichi et al. 1995a). However, not all individual Japanese macaque female ranks follow Kawamura's rules. In a detailed study of female rank in the provisioned Katsuyama group, for example, Nakamichi et al. (1995a) found that about 25% of female-female dyads did not follow Kawamura's rules (Nakamichi et al. 1995a). Deviation from Kawamura's rules was more common in females from medium- and low-ranking matrilines (Nakamichi et al. 1995a). To date, it is unknown if or how physical disabilities influence dominance rank in females.

In male Japanese macaques, who usually immigrate and do not remain in their natal group, kin relationships are expected to be much less important in relation to rank than for females. For males, RHP is expected to be an important predictor of dominance rank (Alberts et al. 2006; Kokko 2013; Parker 1974). In Japanese macaques, age has also been found to be an important predictor of male dominance rank for male (Sprague 1992; Sprague et al. 1998; Suzuki et al. 1998; Takahata et al. 1998), so much so that Sprague characterized dominance rank in terms of the "age-rank structure of troops" (Sprague 1992, p. 437), although the effects of age do vary across populations (Fedigan 1982). For instance, Suzuki et al. (1998) found a linear age-dominance rank relationship in the wild Japanese macaques on Yakushima, with older males tending to be higher ranking, while in the wild Kinkazan group, the relationship was characterized by a humped curve with prime-aged males tending to have higher ranks than younger and old males (Takahashi 2002).

In this study, we examined the influence of physical disability on social dominance rank in adult female and adult male Japanese macaques by addressing the following questions:

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Fig. 8.1 (continued) feet. Gatsu is habitually bipedal in his locomotion; (**d**) and (**e**) Steven (born 1997, index of disability 0.66), an adult male with extensive limb malformations. Steven moves with an uneven quadrupedal gait; (**f**) Monmo (born 2012, index of disability 0.74), a young female with extensive limb malformations on all four limbs, who employs both bipedal and quadrupedal locomotion. She uses a jumping movement in her bipedal locomotion (shown here) and uses her elbows and forearms as weight-bearing surfaces during quadrupedal movement

1. Does the dominance rank of disabled females differ from that of nondisabled females after controlling for expected dominance rank within and among matrilines?
2. How does disability relate to age and dominance rank in adult males in the Awajishima group?

8.2 Methods

8.2.1 Study Site, Species and Group

Data were collected at the Awajishima Monkey Center (AMC), on Awaji Island, Japan. The AMC is a privately operated tourist and education centre, where one large group of free-ranging Japanese macaques (*Macaca fuscata*) is systematically provisioned twice a day with wheat, soy, peanuts, fruit and sweet potatoes. Tourists also feed the monkeys through an enclosure. Provision feeding occurs every day that the monkeys arrive at the AMC (about 10 months of the year); during peak fruiting seasons, the monkeys survive on wild foods almost exclusively and generally do not come to the AMC.

The monkeys at the AMC live in one large group (currently~400 individuals). The group is geographically fairly isolated, so males may leave the group at sexual maturity, live in peripheral all-male groups or disperse individually in the surrounding forest and then reintegrate back into the group as full-grown adults. It is sometimes possible to identify these natal males as returning adults, particularly when they have distinctive limb malformations or when they have remained in peripheral all-male groups that avoid the main group but stay in the general vicinity of the AMC and share at least some of the same home range as the main group. However, for most males in the group, even if it is suspected that they are natal males, kin relationships are unknown. There may be other wild groups in the region; however, these populations are undocumented. Some males, particularly a few extensively disabled males, have remained in the Awajishima provisioned group throughout their lives, although even these males lived around the periphery of the group during their transition to adulthood, only returning to the core of the group as adults (H. Nobuhara and T. Nobuhara, unpublished data). Demographic data, including birth records, as well as kinship and matrilineal information for many identified females, have been collected since the 1960s (H. Nobuhara and T. Nobuhara, unpublished data).

8.2.2 Data Collection

Data on female dominance rank were collected on May–August 2005, 2006 and 2007, as part of a study on adult females and disability at Awajishima (Turner 2010). Data on male dominance rank were collected on June–August 2015, as part of a similar investigation of adult male behaviour and disability. ST recorded all instances of agonistic interactions during 30-min continuous focal animal follows, for both females and males. We analysed only dyadic interactions here. Dyadic agonistic interactions were also recorded ad libitum for focal animals and other individuals who were consistently and reliably recognizable to ST during data collection. We used the following behaviours to estimate dominance relationships: bite, chase, cuff, push, displace, grab, lunge, open-mouth threat, avoid and submissive grimace (Turner 2010).

Our final female data set included dyadic interaction data on 38 females, 12 with CLMs. All disabled females with a disability index score of 0.1 or higher (11 of 12 disabled females; see below) were included as focal animals, and each disabled focal animal was pair-matched in the sample with a female relative who shared as many life history similarities as possible. When a female's kin were unknown or if a female did not have close relatives living, she was pair-matched with a female of similar age and parity in the group (for further information on the focal animal sample, see Turner 2010; Turner et al. 2012). Of the 38 females, ST conducted focal animal sampling on 26, and ad libitum observations were collected on the remaining 12 females in the sample. We analysed 376 dyadic interactions among 195 pairs of females from both ad libitum (~240 field days) and focal data (279 h of focal sample data). There were some changes in group composition over the data collection period; however, there were no major changes in the higher-ranking male or female group members over the period of the study. The overall dominance rank order appeared to be stable during data collection. One female focal animal died during the study, and a different individual was added as a focal animal after her death. Data from both individuals were included separately in this analysis. For two females, we had only two seasons of data, and for two others, we had only one season of data. Because we were interested in the relative rank of individuals, using a sample of females from the population (rather than every adult female in the group) should not greatly influence the rank order outcome. That is, even if the actual order in the group is A > B > C > D > E > F and we only have data on A, B, D and F, in a context such as this where rank is linear, the order will still be A > B > D > F among the known individuals. Using a sample of individuals from the group introduces some unavoidable error into the data, as does having pairs with no recorded interactions. In a large group like that at Awajishima, which is known for being more tolerant and less despotic than usual for Japanese macaques, many individuals may simply avoid interacting with one another rather than engaging in direct contests (Fedigan 1982; Kaigaishi et al. 2016; Nakamichi and Yamada 2010). Our data show less certainty in relation to the specific order of females who are closely ranked in the dominance order compared to the certainty associated with the overall dominance order; this aspect of our results likely reflects a combination of behavioural factors (a less despotic, large group where individuals can often avoid conflict) and having individuals in the group missing from the analysis.

We collected data on all males who were central to the group during the period of data collection. Our final male data set included dyadic interaction data on 22 adult males, 8 of which had CLMs. Of the 22 males, ST conducted focal animal sampling on all but 1 (140 h of focal sampling data from ~85 field days, with ad libitum sampling on the remaining individual). Behavioural data collection yielded

95 dyadic interactions among 62 pairs of individuals. For the males, TN and HN also conducted 136 structured food tests among 82 different pairs of individuals, in which a peanut was placed between two adult males[1] and we recorded which monkey took the peanut and other details of their interactions. For a subset of pairs (23 pairs of individuals), we had data from both "peanut tests" and behavioural observations (with a total of 82 associated interactions, 42 of which were from peanut tests). The direction of winner-loser interactions was consistent between peanut tests and observed behaviour in 100% of cases. We therefore amalgamated the peanut test data and the observational data for the males, for a total of 231 dyadic interactions among 119 different pairs.

8.2.3 Potential Predictors of Dominance Rank

8.2.3.1 Disability

For all individuals with congenital limb malformations, we collected detailed photographic records and written descriptions of their individual hand, foot and limb anatomical structures. We then used an index of disability developed for this population to obtain a 0–1 score to measure the extensiveness of an individual's congenital limb malformations, where 0 corresponds with no limb malformations and 1 corresponds with the absence of all 4 limbs (Turner et al. 2008). The index of disability accounts for both absence and malformation in limbs and digits. The index is weighted to account for disability in the following ways: absence is given more weight than malformation; hands are given more weight than feet and thumbs more than other digits.

8.2.3.2 Age of Males

We used available demographic data from Awajishima (H. Nobuhara and T. Nobuhara, unpublished data) to classify individuals according to age. When exact age was unknown, we estimated the age of adult males by comparing physical characteristics with males of known age at Awajishima and by using published age-related physical markers from various Japanese macaque groups (Hamada and Yamamoto 2010). We used characteristics such as body size and shape (younger males are less robust), facial skin, degree of scarring, scrotal development and colour and signs of old age such as shorter or stiffer gait, tremors and tooth loss (Hamada and Yamamoto 2010; Takahashi 2002). We knew the birth year for 8 of 22 of the males in our sample, with known ages ranging from 10 to 26 years at the time of data collection. There was at least one of these reference males of known age for each age group we created. We grouped the males in our sample into five age classes:

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[1] Six of the interactions among the females were also observed during informal "peanut tests" that TN and HN conducted spontaneously during provision feeding.

1. Young adult males (males around 10 years old (9–11 years)): these were the youngest adults, with most males in this category being 10 or 11 years; however, as we were estimating, it is possible that the sample contained a 9-year-old. Ten years is usually the age at which males are considered fully adult in Japanese macaques (Hamada and Yamamoto 2010); however in some studies, males are considered adult from around 7 years of age (Inoue and Takenaka 2008).
2. Young prime-aged males: males around 13 years old (12–14 years).
3. Prime-aged males: males around 17 years old (15–19 years), full-sized adults, both in terms of limb length and apparent body weight.
4. Old males: males around 21 years old (20–23 years).
5. Very old males: males around 25 years old, showing strong signs of aging, with stiff, tottering gait, some apparent loss of muscle mass and often some tooth loss.

8.2.3.3 Kinship and Matrilineal Relationships Among Females

As discussed in the introduction, kinship is known to have a strong influence on female dominance rank in Japanese macaques. Using kinship records from the Awajishima Monkey Center (e.g. grandmother, mother, sister and aunt relationships are known for many females; H. Nobuhara, T. Nobuhara, S. Turner and Y. Kaigaishi, unpublished data), we were able to create an expected rank order within each matriline based on Kawamura's rules (Kawamura 1958). We normalized this expected within-matriline rank on a scale from 0 to 1 and used it as a predictor of rank in our statistical model. Three females without known relatives were given the overall mean position for expected within-matriline rank. It had not been previously confirmed that this population follows Kawamura's rules (Nakamichi and Yamada 2010), as the AMC group is reported as less despotic and more tolerant than other groups of Japanese macaques (Inoue-Murayama et al. 2010; Kaigaishi et al. 2016; Koyama et al. 1981; Nakamichi and Yamada 2010). However, we do know that kinship is important in their relationships and could assume that it was likely that Kawamura's principles did apply to this group.

Kin relationships over time in the group should also lead to an overall rank order among matrilines (Koyama 1970). The resulting matriline rank order should then predict individual rank, such that females within the same matriline are expected to be close together in the overall dominance rank order and individual members of higher-ranking matrilines are expected to outrank members of lower-ranking matrilines. However, historical kin relationships in this group are not known well enough to determine an expected rank order among matrilines. Since we did not have an independent measure of the order among matrilines, we controlled for the effect of among-matriline order on individual rank by creating a blocking variable derived from the data. After establishing the most likely overall dominance rank order, we calculated the mean dominance rank among individuals within each matriline and ordered these means sequentially to create an overall rank order for the matrilines. The resulting among-matriline rank order was also normalized on a scale from 0 to

1 and used as a predictor variable in the statistical model. This derived variable effectively centred each individual rank on its matriline average, to better fit the model to known sources of biological variation.

This resulted in two independent variables in the statistical model that we used to represent the expected effect of kin relationships on individual rank order: (1) among-matriline order (derived from the data and therefore used only to control for this known biological effect) and (2) expected within-matriline order (based on Kawamura's rules and independent AMC records of kin relationships within each matriline).

8.2.4 Analysis

8.2.4.1 Assessing Dominance Probabilities Using the Percolation-Conductance Method

We calculated female and male dominance rank order separately using directional dyadic agonistic interactions and inverse submissive interactions between known pairs of same-sex individuals. It is important to note that although individual male Japanese macaques are generally dominant over individual female Japanese macaques, some high-ranking females are individually dominant over some males (Fedigan 1982). In particular the highest-ranking female in the Awajishima group was observed to win dyadic food tests with numerous males, including the second highest-ranking male in the group. However, because the behavioural data sets were collected in conjunction with broader sex-specific studies that were separated in time (females 2005–2007 and males 2015), we were unable to quantify and examine the degree to which the sex-specific dominance hierarchies overlapped.

For each sex, we entered behavioural data into a win/loss interaction matrix and then used the percolation-conductance method to create a matrix of dominance probabilities and estimate the best dominance rank order to represent the data. For this analysis, we used the Perc package in R (Crawley 2007; Fushing Lab and McCowan Lab 2015). The percolation-conductance method uses the direct win/loss interactions to generate indirect pathways among individuals. For example, if we know that A > B, B > C and C > D, through indirect pathways, we can estimate information about A's relationships to C and D. The information gained from the indirect pathways is weighted in the model according to the estimated reliability of that information. This method uses a combination of direct win/loss data and the indirect pathways to estimate dominance probabilities among individuals in the matrix and to model the most probable dominance rank order. Through performing a repeated series of random walks (1000 permutations), the percolation-conductance method estimates a series of hierarchies (10) and determines the most likely hierarchy among the series by quantifying the pathway cost associated with creating each hierarchy (Fushing Lab and McCowan Lab 2015).

In the female data set, there were many missing cells in the original matrix, a constraint which had previously limited our analysis of rank order (Turner et al. 2014). The percolation-conductance method allowed us to make full use of the data we had available for the females, in order to examine the possible influence of disability on dominance rank order among females in this population. This method does not assume linearity of the dominance hierarchy. It also provides a visual assessment of the uncertainties associated with different parts of the dominance hierarchy (Fushing Lab and McCowan Lab 2015).

8.2.4.2 Statistical Analyses

We analyzed the relationship among dominance rank order, disability, and kinship (for the females) and dominance rank order, disability, and age class (for the males), using linear regression. In the female regression models, we used linear rank order as the dependent variable with three independent predictors: (1) disability category (disabled or not; analysis 1) or disability index (analysis 2), (2) expected within-matriline rank predicted by Kawamura's rules, and (3) mean rank order for each matriline (we used this as a model offset to account for differences among matrilines, effectively centring each individual rank on its matriline average). In the male regression models, we used linear rank order as the dependent variable with two independent predictors: (1) disability category (disabled or not; analysis 1) or disability index (analysis 2) and (2) age category.

We visually checked quartile plots for normal distribution of residuals and plotted the residuals against the fitted values to check for equality of variance. We then removed non-significant interaction terms and non-significant factors. We chose the final model using the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) to determine which model was best able to explain the variance in the data.

8.3 Results

8.3.1 Estimates of Female Dominance Relationships

In the original female win/loss conflict matrix, the relationships were very linear (205 transitive triangles and 3 intransitive triangles, yielding a transitivity measure of 0.985 and an alpha of 136.2). We were able to use the maximum length of six indirect steps in the model to bootstrap our data, as the addition of each new level of indirect pathway continued to increase the reliable data available. The percolation-conductance method generated ten versions of the dominance rank order, and although these estimated dominance rank orders varied somewhat, with small permutations in individual rank order in the parts of the matrix that contained the highest levels of uncertainty, the overall order was robust,with low levels of uncertainty (Fig. 8.2).

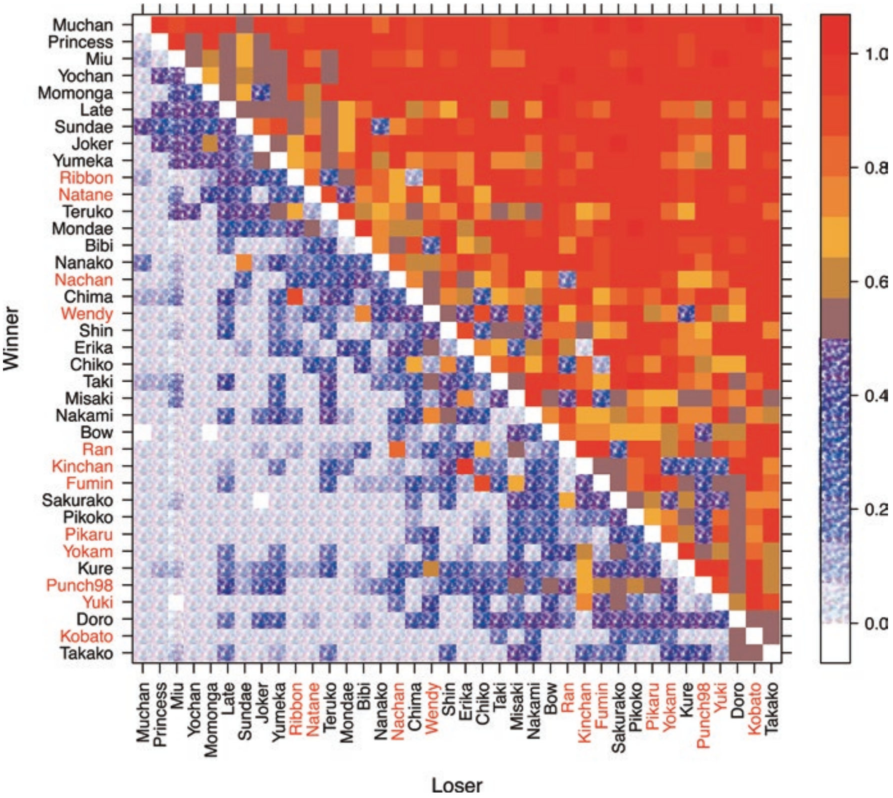

Fig. 8.2 Final female dominance rank probability matrix. The females are ordered from highest (top of Y-axis) to lowest ranking (bottom of Y-axis). Names highlighted are disabled females. The heat map shows the degree of certainty in the dyadic level dominance relationships (individual cells) and the overall pattern of certainty for the dominance rank order. The white squares on the diagonal indicate the intersection of the row and column for the same individual. Values close to 1 indicate a high probability that the individual in the row outranks the individual in the column, whereas values close to 0 indicate a high probability that the individual in the row is subordinate to the individual in the column. Values close to 0.5 indicate a high level of uncertainty with respect to the dominance relationship between two individuals. The degree of certainty is lowest close to the centre line, while further from the centre line, the degree of certainty for relationships increases, suggesting that the overall dominance rank probabilities are quite certain, while there is generally less certainty associated with the exact order of individuals who are closely positioned in the estimated dominance rank order

8.3.2 Predictors of Female Dominance Rank

If disability had a strong negative effect on female dominance rank, we would expect disabled females to hold relatively low-rank positions. While disabled females were distributed throughout most of the dominance rank order, more females occupied positions near the bottom of the dominance rank order (Fig. 8.3). Taking into account matrilineal kinship relationships, both within matrilines and

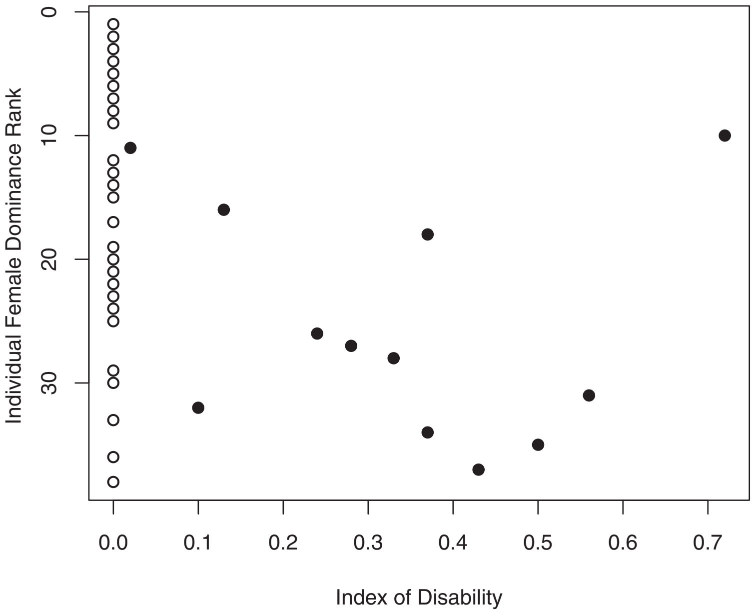

Fig. 8.3 Individual female dominance rank, where 1 and 38 correspond to the highest and lowest ranks, respectively. The open circles represent the dominance rank of individual nondisabled females. The filled circles show the dominance rank order and the extent of physical impairment as measured by our index of disability; for example, the most extensively disabled female in the group holds the tenth position in our estimated dominance rank order

among matrilines, the results of our final linear model confirmed that Kawamura's rules significantly predict female dominance rank order in the Awajishima group (linear regression: d*f* = 34, adjusted *R*-squared = 0.78, $t = -3.52$, $p = 0.001$). Our model also showed that disability had an independent and significant negative influence on dominance rank order for females in the Awajishima group (linear regression (using disability category), d*f* = 34, adjusted *R*-squared = 0.79, $t = 2.89$, $p = 0.007$; (using index of disability), d*f* = 34, adjusted *R*-squared = 0.78, $t = 2.56$, $p = 0.015$; Fig. 8.4).

8.3.3 Estimates of Male Dominance Relationships

We were able to estimate a male dominance rank order with a high degree of certainty. Male-male relationships were highly linear (227 transitive triangles and no intransitive triangles, yielding a transitivity measure of 1 and an infinite alpha), and

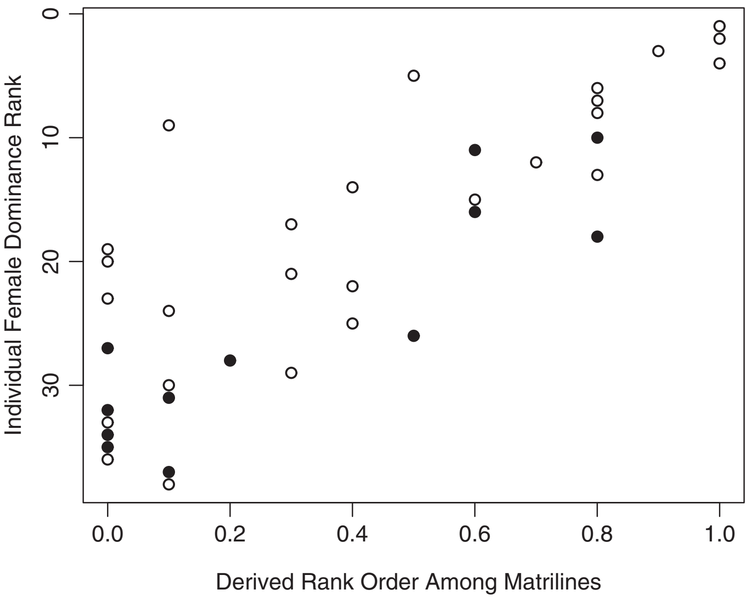

Fig. 8.4 Individual female dominance rank (from 1 to 38) and observed within-matriline rank plotted as a function of the derived matrilineal rank order. Each of the 11 matrilines is separated by 0.1 on the horizontal axis, and the matrilines are ordered according to the mean rank of females within each matriline. Filled circles show disabled females, and open circles show nondisabled females, with the highest ranked adult female in the top right corner of the figure and the lowest ranked adult female near the bottom left corner of the figure. Disabled females tended to be somewhat lower ranking than expected within their matrilines

because the addition of each new level of indirect pathway continued to increase the reliable data available, we were able to use the maximum length of six indirect steps in the model to bootstrap our data in order to increase the information available for deriving dominance estimates. This process resulted in the model producing a consistent most probable dominance rank order for the adult males at AMC (Fig. 8.5).

8.3.4 *Predictors of Male Dominance Rank*

Disabled males were interspersed throughout the dominance rank order (Fig. 8.6). In our final model, neither the presence/absence of congenital limb malformations nor the severity of disability showed a significant association with dominance rank in males (linear regression (using disability category), d*f* = 19, $t = -1.375$, $p = 0.185$; (using index of disability), d*f* = 19, $t = -0.928$, $p = 0.365$). Age class, however, was significantly and positively associated with dominance rank such that older males tended to hold higher positions in the dominance rank order (linear regression: d*f* = 20, adjusted *R*-squared = 0.50, $t = -4.688$, $p = 0.0001$; Fig. 8.7).

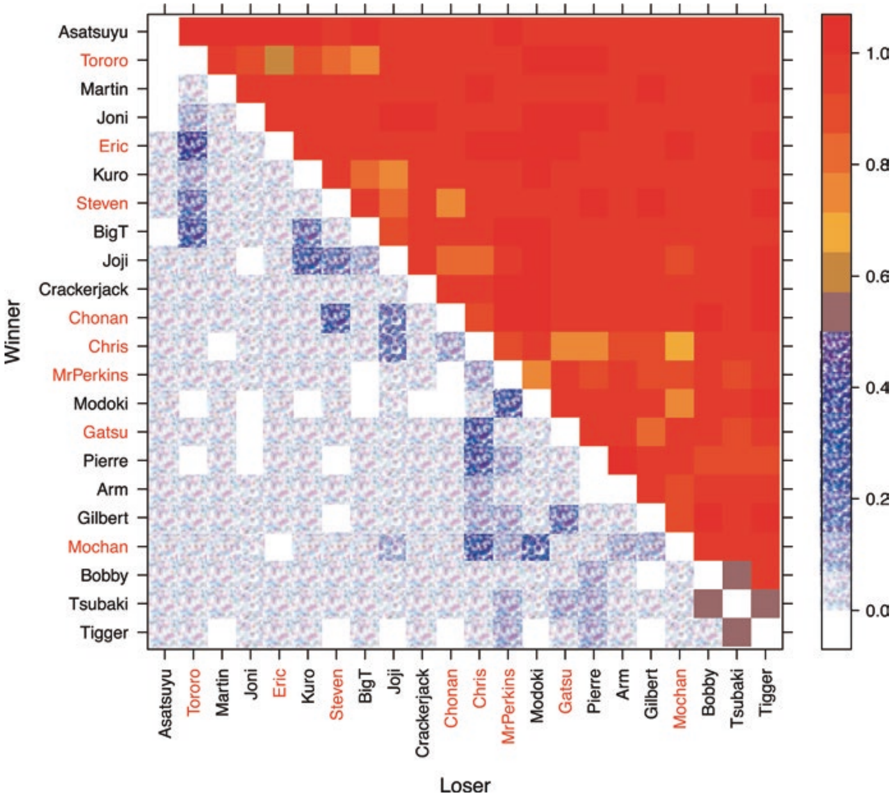

Fig. 8.5 Final male dominance rank probability matrix. The males are ordered from highest (top of the Y-axis) to lowest ranking (bottom of the Y-axis). Names highlighted are disabled males (e.g. Tororo, Eric etc.). The heat map shows the degree of certainty in the dyadic level dominance relationships (individual cells) and the overall pattern of certainty for the dominance rank order. The white squares on the diagonal indicate the intersection of the row and column for the same individual. Values close to 1 indicate a high probability that the individual in the row outranks the individual in the column, whereas values close to 0 indicate a high probability that the individual in the row is subordinate to the individual in the column. Values close to 0.5 indicate a high level of uncertainty with respect to the dominance relationship between two individuals

8.4 Discussion

Among adult female Japanese macaques at Awajishima, disability had a significant negative influence on dominance rank order. However, disabled females were not all low ranking; rather they were spread throughout most of the hierarchy (Fig. 8.3). For example, the most physically disabled female in the group held the tenth highest position in the rank order (Ribbon: index of disability 0.72; Fig. 8.8). Once we controlled for matrilineal kinship using Kawamura's rules, both disability and degree of severity of disability did significantly predict female dominance rank. Although disabled infants are less likely to survive their first year of life compared to

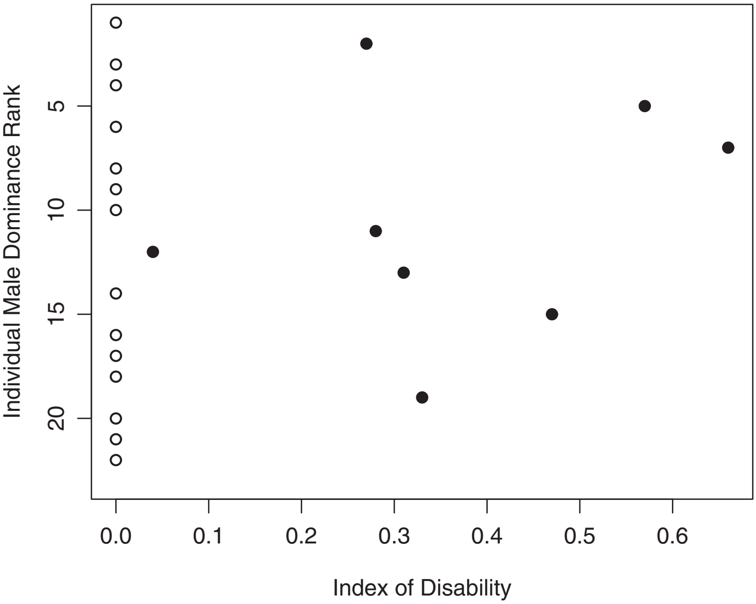

Fig. 8.6 Individual male dominance rank where 1 and 22 correspond to the highest and lowest ranks, respectively. The open circles represent the dominance rank order of individual nondisabled males. The filled circles show the dominance rank order and the extent of physical impairment as measured by our index of disability

nondisabled infants (Nakamichi et al. 1997), we have previously documented few behavioural costs associated with disability in this group (Turner et al. 2012, 2014). The results of this current analysis suggest, however, that lower dominance rank represents such a cost for disabled adult females.

Although disabled females seemed to maintain at least some of the overall rank of their matriline, they were somewhat lower ranking than expected in relation to their own kin. It is possible that while their kin supported them in agonistic interactions with non-kin, nondisabled kin were simultaneously taking advantage of their relatives' lower resource holding potential (RHP) to increase their own dominance rank within their matriline. At no time during the 9 months of data collection did we observe rank reversals, however, and disabled females did not receive more agonism, and received less bite and chase agonism, than nondisabled females (Turner et al. 2014). Consequently, the mechanism and timing of disabled females attaining their individual positions in the rank order remain unclear. Experimental research on Japanese macaque rank acquisition suggests that individual ranks were likely established when females were young and were likely influenced by availability of mothers and close kin for support and alliances (Chapais 1988a, b). It is possible that maternal disability, and/or the disability of close kin, may influence these dynamics at AMC; however, our sample of disabled mother-daughter pairs was too small to examine this possibility statistically.

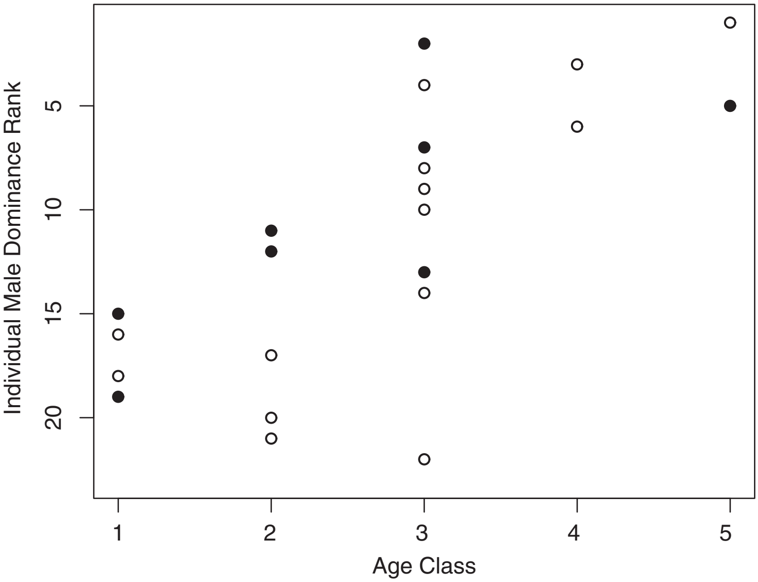

Fig. 8.7 Individual male dominance rank, age class and disability. Males were classified from youngest (1) to oldest (5). Overall, older males held significantly higher dominance ranks than younger males. Disabled males were found across age groups and throughout the dominance rank order. Open circles represent nondisabled males, and filled circles represent disabled males

Fig. 8.8 Disabled monkeys engaged in agonism and dominance-related interactions in the AMC group. Here, Ribbon, the extensively disabled adult female (index of disability 0.72), who held the tenth position in the most probable dominance rank order constructed using the percolation-conductance method for the female data set, lunges and open-mouth threatens another monkey

In previous research, we found that disabled females tended to be less social than nondisabled females across a number of measures, such as number of social partners they affiliated with, and time spent engaged in social behaviours, such as grooming (Turner et al. 2014). We also found that this difference in social behaviour between disabled and nondisabled females was likely not the result of disability-associated bias in the selection of social partners but more likely reflected disabled individuals' need for more resting time (Turner et al. 2014). Another possible explanation for the results of our current study is that lower dominance rank among disabled females emerged from their lower overall engagement in social time and activities. However, though statistically significant, the differences in the social interactions of disabled females were relatively small, and disabled females do engage in agonism and dominance-related interactions (Fig. 8.8), biting and chasing other females at rates that were not statistically different from those of the nondisabled females in our study (Turner et al. 2014).

Among adult males, we found no evidence to suggest that the presence of disability or the severity of disability carried a cost in terms of dominance rank. Disabled males held ranks throughout the dominance hierarchy, and there was no statistically significant relationship between dominance rank and disability. In particular, the second highest-ranking male had moderate manual disabilities (Tororo, index of disability = 0.27), and males holding the fifth rank (Eric, index of disability = 0.57) and seventh rank (Steven, index of disability = 0.66; Fig. 8.1d, e) were both extensively disabled. We found that age class explained a large proportion of the variance associated with rank order among the adult males, with the oldest males holding the highest ranks in the dominance hierarchy. Although we found no significant interaction between age and disability in our model, it is possible that there is an indirect connection between disability and age, via the length of tenure in the group. We did not have an independent measure of length of tenure in the group, but anecdotal evidence suggests that longer tenure was also associated with higher rank and age at Awajishima (H. Nobuhara and T. Nobuhara, unpublished observations). This pattern has been observed in other rhesus and Japanese macaque groups (Manson 1995; Sprague 1992; Sprague et al. 1998). For males, length of tenure in the group may be a key determinant of dominance rank (Suzuki et al. 1998; Takahashi 2002) and if so, likely hinges on the social relationships and knowledge built in the group over time.

It is also possible that disabled males are more likely to remain in the natal group than nondisabled males, leading to longer-than-average tenure. Anecdotally, we know of cases where disabled males never completely left the group. However, it is difficult to compare these cases directly with the emigration and immigration behaviour of nondisabled males because the disabled individuals are more easily individually identifiable over time due to their unique limb configurations, and without further data, it is thus impossible to rule out associated sampling biases (H Nobuhara and T Nobuhara, unpublished data). Tenure in the group and associated social benefits may explain some of the variation in dominance rank among males and may help explain the presence of disabled males throughout the dominance rank order; however, the complexities of these relationships remain to be evaluated.

Our results suggest that RHP may not be a consistent predictor of dominance rank in male Japanese macaques at Awajishima, a suggestion also supported by research on other groups. In wild male Japanese macaques at Yakushima, most rank changes were not the result of fights among males; instead, emigrations and death of high-ranking males were responsible for 95% of male rises in rank, and 81% of drops in rank were the result of males immigrating into the group into a higher position in the hierarchy (Suzuki et al. 1998). In some groups of Japanese macaques, such as the wild group on Kinkazan Island, old males tended to decline in rank, with age showing a humped curve-shaped relationship, such that males in their physical prime held the highest rank positions (Takahashi 2002). However, in the free-ranging Katsuyama group, Nakamichi et al. (1995b) described a case of a very old male who maintained his alpha status through coalitions with high-ranking females, despite deterioration in his ability to walk. In the Awajishima group, three different old males have held the alpha position over the last decade.

How are old and/or disabled males able to hold high rank? Why would younger, nondisabled males not fight to increase their rank over old and/or disabled males? The strength and direction of the relationship between dominance rank and reproductive success are arguably a key element in answering these questions. While high rank can have a strong and positive association with reproductive success (e.g. Alberts et al. 2006; Jack and Fedigan 2006; Majolo et al. 2012), the relationship is variable and not always positive (Berard 1999; Berard et al. 1993; Majolo et al. 2012; Manson 1992, 1995; Widdig et al. 2004). In the free-ranging group of Japanese macaques at Arashiyama, for instance, Inoue and Takenaka (2008) found that length of tenure in the group, which was positively associated with high dominance rank, had a strong but negative influence on paternity rates. When high rank does not carry a benefit in terms of reproductive success, the potential individual costs of attempting to improve rank may not outweigh the benefits (e.g. risk of injury or risk of being chased out of the group by a coalition of conspecifics). Serious one-on-one fights are rare at Awajishima, perhaps reflecting a situation where there is little reproductive benefit to be gained by such encounters.

As disability showed no connection to dominance rank in adult males in our study, our results underscores the importance of examining multiple factors potentially associated with rank and reproductive success when studying dominance rank, e.g. age (as found in this study); ecological and seasonal variables; length of tenure in the group; group behavioural conventions; cognitive performance; personality and formation of coalitions (Fedigan 1982; Nakamichi et al. 1995a; Nakamichi and Yamada 2010; Reader and Laland 2001; Suzuki et al. 1998; Takahashi 2002); as well as female choice, sperm competition, and the relationship between mating success and paternity success in males (Alberts et al. 2006; Alberts et al. 2002; Berard 1999; Berard et al. 1993; Bercovitch and Berard 1993; Manson 1992, 1995; Ostner et al. 2008; Widdig et al. 2004). In particular, as Fedigan (1982) wrote, "adult primates are…strongly influenced and constrained in their behaviour by the behaviour of other group members", and she emphasized that "alliances and coalitions have a strong, even overriding, impact on conflict outcome" (p. 107). When alliances and coalitions occur, individual one-on-one fighting ability becomes less important in determining outcomes. Recent field experiments on cooperative tasks suggest that the monkeys in the Awajishima group may be more tolerant and inclined to cooperate than is typical for Japanese macaques (Kaigaishi et al. 2016). Such cooperation may decrease the importance of RHP as a predictor of rank in this group and increase the likelihood of coalition and alliance formation, although this possibility remains to be investigated.

Finally, recent research has emphasized the importance of endogenous, self-organization properties of dominance relationships (Dey and Quinn 2014). Dey and Quinn (2014) argued that processes that act independently from individual attributes have more influence on the formation and maintenance of dominance hierarchies than have previously been recognized. These processes include such variables as winner and loser effects (Dey and Quinn 2014), priority of "ownership" of a resource (Kasumovic et al. 2010; Kokko 2013) and particular species or group-specific social conventions (Kokko 2013).

Linda Fedigan's analysis of dominance and her application of this concept in primatology is still relevant more than 30 years after the publication of *Primate Paradigms: Sex Roles and Social Bonds* (1982). Early on, she recognized that dominance was not just about physical strength and aggression but involves a multitude of complex factors and social dynamics. As Fedigan described:

> Obviously it helps an individual in a general sense to be physically well and strong, but the power of social learning and social tradition is so pervasive in primates that it often overrides the importance of physical factors in determination of dominance rank. (Fedigan 1982, p. 102)

This was a particularly important insight at a time when many researchers were treating dominance as an immutable trait inherent to the individual, which was more important for males than females, and fundamentally about physical size and strength. The Japanese macaques of Awajishima, many of whom have extensive physical impairments, illustrate the importance of not overemphasizing physical attributes, to the exclusion of other factors, in our investigations of social dominance rank relationships.

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