Introduction

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Bordering the western side of Kyoto, the ancient capital of Japan, is a picturesque little town called Arashiyama (嵐山: stormy mountain). Nestled at the foot of the mountains bordering Kyoto city, it has been the subject of many artists' brush and pen. Perhaps it is most famous for Togetsukyo bridge, which crosses over the Hozu river at the point where it flows out of the mountain range. This scenic area is often depicted on contemporary postcards and many Edo period woodblock prints. It is, and always has been, a popular area for local and international tourists.

Less known, is the world that exists in the mountains above, with its near vertical slopes densely forested with towering hardwoods and pines. In this world there is a group of inhabitants living in a very complex society bound by rules. They are colloquially referred to simply as 'saru' by most Japanese, but are known technically as the 'Nihonzaru' or Japanese monkeys (*Macaca fuscata fuscata*). Their human-like qualities and emotions have been the subject of many anthropomorphic legends, folktales and paintings. However, it was not until after the end of World War II that attempts were made to systematically observe these animals and to unravel the mysteries concerning their human-like attributes, or as some may argue, our own monkey-like behaviour. The monkeys of Arashiyama were one of the first primate groups to receive scientific attention by primatologists in Japan, and indeed in the world.

The Arashiyama group of Japanese macaques holds a distinguished place in primatology as one of the longest continuously studied non-human primate populations in the world. Habituation of the Arashiyama-Kyoto macaques and informal observations began in 1948 by school teacher Eiji Ohta and later by Junichiro Itani and others in 1951. Systematic data collection and habituation with provisioning by Japanese primatologist, Naonosuke Hazama, followed in 1954 and the first scientific publications pertaining to the Arashiyama macaques appeared in the early 1960s. Non-Japanese researchers began working at the

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site in the late 1960s and since that time Arashiyama has been the focus of numerous international collaborative research efforts.

In 1972, a subgroup of the Arashiyama population was transferred to south Texas in the USA where they live under semi-free ranging conditions and where research by non-Japanese primatologists continued until 1999. They became known as the 'Arashiyama West' population of Japanese macaques. In 1984, a subgroup of the Texas population was, in turn, translocated to the University of Montréal, Canada, where they were studied until 1998. Since demographic data have been continuously collected for the Arashiyama-Kyoto population, these monkeys represent unique resources for behavioural studies that are contingent on individual identification and known genealogical relationships. The value of this longitudinal dataset cannot be overstated as it has allowed researchers to move far beyond cross-sectional studies and tackle larger issues pertaining to individual, matrilineal and group histories. Important scientific findings have been derived from this longitudinal collaborative research on such topics as kinship, group fission, behavioural traditions and male transfer, as well as reproductive and non-reproductive sexual behaviour. Taken together, research at Arashiyama has made a significant and enduring contribution to the discipline of primatology, and more broadly, to the study of animal behaviour and human evolution.

The present edited volume covers research on the Arashiyama troops since the publication of Fedigan and Asquith's 1991 volume, *The Monkeys of Arashiyama: Thirty-five Years of Research in Japan and the West* (State University of New York Press). Like Fedigan and Asquith's book, this volume takes advantage of the long-term data available from years of collaborative research between observers working at Arashiyama. It includes 19 chapters by a variety of Japanese and international researchers. Three chapters include short box essays that relate to the chapter's topic. Contributions fall into four main categories: (1) Historical perspectives; (2) Sexual behaviour; (3) Cultural behaviours, social interactions and ecology; and (4) Management and education.

At the beginning of the 'Historical perspectives' section, Huffman, Fedigan, Vasey and Leca (chapter 1) provide a brief timeline of six decades of research activities on the Kyoto, Texas and Montréal populations of Arashiyama macaques. This chapter is then followed by a few English translations of Japanese essays written by pioneers involved in the early efforts to study the Arashiyama-Kyoto troop of Japanese monkeys. These essays provide the reader with a sense of the human drama behind early research at Arashiyama and a glimpse of the early days of primatological research in Japan. This is the first time any of these accounts have appeared in English. Chapter 2 and chapter 4 were both originally written in Japanese for a more general audience to showcase the pioneering efforts that contributed to making this site an important starting point for primatology.

The author of the first essay (chapter 2), Mr Eiji Ohta (born *c*. 1928) was an educator and a founding member of the Arashiyama Natural History Society, a group of local naturalists, primatologists and community members who promoted research and education at Arashiyama for many years. Ohta provides a detailed account of his first encounters with the monkeys of Arashiyama and the accidental destruction of the first research station at this field site. Chapter 4 was written by Kyoto University Professor Emeritus Naoki Koyama (born 1941), who elucidated, in collaboration with Sophia University Professor Emeritus Koshi Norikoshi (born 1941), the influence of matrilineal kin relationships on incest avoidance and group restructure after troop fissioning. Koyama's essay is based on the first detailed studies of primate troop fission and underscores the importance of individual recognition in conducting such research. The third essay (chapter 3) is an account of research activities at Arashiyama during the late 1950s and was written especially for this volume by Kyoto University Professor Emeritus Yukimaru Sugiyama. He spent one season at Arashiyama, before moving on to study Japanese monkeys at Takasakiyama, on the island of Kyushu, langurs in India and chimpanzees in East and West Africa.

The following chapters are based on quantitative and qualitative research. Chalmers, Huffman, Koyama and Takahata (chapter 5) present an unprecedented 50-year record of life-history traits (e.g. age-specific reproductive parameters, infant survival and mortality) among 200 female Japanese macaques from 14 matrilines, all members of the Arashiyama-Kyoto troop. Their chapter emphasises the characteristics of long-lived individuals (i.e. >25 years). Extending from 1954 to 2007, this dataset complements and enhances Koyama *et al*.'s (1992) report, which analysed the demographic parameters of all troops feeding at the Arashiyama site from 1954 to 1983. The authors urge for a continuation of such long-term studies at this field site to better understand the various female life-history traits, and more particularly those of the very old individuals. In most of the subsequent chapters, researchers and educators capitalise on these valuable longitudinal demographic data to address various questions related to a wide range of behavioural research, as well as population management, and public education. Key features of these longitudinal demographic data include the systematic identification of all group members and detailed knowledge of genealogical relationships in the Arashiyama-Kyoto population, but also in the subgroups translocated to the USA (Arashiyama West troop) and Canada (Montréal troop).

In the second section of the volume, entitled 'Sexual behaviour', Huffman and Takahata (chapter 6) use records collected at Arashiyama by several researchers, including themselves, to investigate the possible existence of long-term mating preferences in male and female Japanese macaques over their reproductive lifetimes. They argue that the best mating strategy for high-ranking males is to

mate preferentially with high-ranking and mid-aged females because this may ultimately result in higher reproductive success. However, after considering various factors, such as age, dominance rank and maternal kinship, they show that both males and females change mate selection patterns over the course of their life, as a consequence of their life-history trajectories and variation in their social status. While females tend to seek novelty, males, in contrast, seek familiarity and perhaps, in turn, social stability within the troop through their associations with adult females. Huffman and Takahata's findings shed further light upon our understanding of the relative roles of both sexes in the maintenance, and ultimate evolution, of mating systems.

In chapter 7, O'Neill examines the relationships between behavioural and endocrine changes during the ovarian cycles of female Japanese macaques in the Arashiyama West colony. She provides a detailed analysis of female preconceptive and post-conceptive reproductive behaviour, as well as same-sex sexual behaviour, in relation to hormonal variation over the course of the female reproductive cycle. Her study reveals cyclic patterns in reproductive sexual behaviour by females, with significant increases in attractivity (e.g. mounting and holding behaviour received from males) and proceptive behaviours (e.g. mounting, holding and other sexual behaviours directed toward males) during the follicular and periovulatory phases of the cycle, followed by a complete absence of these behaviours during the luteal phase. Functionally, these behavioural changes may serve to locate and attract males who will then be in place for mating when ovulation does occur. Her demonstration of a similar relationship between homosexual behaviour and endocrine condition supports the argument that, although non-reproductive, same-sex mounting in Japanese macaque females is primarily sexual in motivation. O'Neill's research also provides evidence for the reliability of faecal analysis and enzyme immunoassay techniques for evaluating the hormonal status in Japanese macaques.

In chapter 8, Jack describes and explores the mating strategies and behaviours of male Japanese macaques living in the Arashiyama West colony, in order to determine how these affect their ability to attract and gain access to female mates. Using a stepwise regression analysis, she tests the influence of male rank, age, spatial distribution, affiliative and aggressive interactions with females, and display performance on male mating strategies. Her results show that male age, affiliation and aggression are significant variables, and together explain a substantial proportion of the observed variation in males' mating frequency score (MFS). The negative correlation between male age and MFS may reflect female aversion to mates from preceding years and is likely the result of limitations on male dispersal at the Texas site. High rates of affiliation and aggression may be the by-product of increased proximity between males and females during the mating season. However, given the rarity of male to

female aggression during the non-mating season, Jack argues that the significant correlation between male aggression and MFS may indicate that males are employing a form of sexual coercion to acquire mating opportunities.

In chapter 9, Pavelka and Fedigan tackle the hypothesis that natural selection has favoured the cessation of reproduction in female monkeys and apes who are grandmothers because the benefits of caring for grandchildren outweigh the benefits of continuing to produce more babies. To do so, they employ a large dataset on Arashiyama West female Japanese macaques and review their work on the costs and benefits of reproduction in old age versus post-reproductive grandmothering. Their results show that post-reproductive grandmothers are extremely rare in this population, but when present, they increase their grandchild's chance of surviving to age one. They suggest that the cessation of reproduction in these females is a by-product of selection favouring longevity rather than as a result of direct selection for reproductive termination. The new data they present here further support the view that reproductive costs do not appear to increase with age. They argue that continuing to reproduce until death is beneficial, not costly, to the fitness of Arashiyama West female Japanese macaques. Overall, Pavelka and Fedigan's findings provide considerable insight into the evolution of menopause in humans.

The last three chapters of this section focus on non-conceptive sexual behaviour. First, Vasey and VanderLaan (chapter 10) review some of their long-term research on female homosexual behaviour in the Arashiyama-Kyoto macaques. In this troop, a substantial proportion of females routinely engage in same-sex mounting and courtship within the context of temporary, but exclusive, sexual relationships that are virtually identical to those found in heterosexual consortships. Although numerous sociosexual hypotheses have been tested to account for such female–female sexual behaviour in Japanese macaques, none has been supported. Vasey and VanderLaan review evidence pertaining to female–female courtship, mount postures, pelvic thrusting and genital stimulation and conclude that these behaviours can be primarily, and objectively, described as 'sexual' in character. They argue that female homosexual behaviour in the Arashiyama macaques has broad implications for mating system dynamics because males must not simply compete intra-sexually for access to female mates, but they must do so *inter*-sexually as well. In a related essay, Takenoshita (box 10) provides a descriptive account of male Japanese macaque homosexual behaviour at Arashiyama, and discusses a series of possible proximate and ultimate explanations for this seldom observed behaviour.

In chapter 11, VanderLaan, Pellis and Vasey address the question of why same-sex sexual behaviour is so widespread among members of the Arashiyama-Kyoto macaque population. In addition to adult homosexual behaviour, juvenile males frequently mount one another. The authors first describe how juvenile

male–male mounting is often associated with social play and more generally with tension reduction. They go on to propose a developmental model of how male–male mounting progresses through the juvenile stage and gives rise to adulthood patterns of non-conceptive mounting. The chapter closes with consideration of the biogeography and evolution of adult female–male and female–female mounting in Japanese macaques. In essence, the authors provide a springboard for further study into these puzzling phenomena and how they may vary in frequency and form among populations across the Japanese archipelago.

To conclude this set of chapters about non-conceptive patterns of sexual behaviour, Inoue (chapter 12) examines the contexts of male masturbation in Japanese macaques at Arashiyama, and investigates possible mechanisms and functional aspects of the behaviour. His results are consistent with the hypothesis that males masturbate more frequently when opportunities to copulate are rare. Inoue speculates that male masturbation does not negatively affect reproductive success and may actually function to increase sperm quality because the next ejaculate may contain fewer, but quicker-moving sperm. Taken together, this work underscores the important point that masturbation, when it is adaptive, likely serves different functions depending on the species in question.

The third section of the book compiles comparative, longitudinal and experimental studies on cultural behaviour, social interactions and feeding ecology of the Arashiyama macaques. In chapter 13, Leca, Gunst and Huffman examine one of the most thoroughly documented behavioural traditions in non-human primates, namely, stone-handling behaviour in the Arashiyama-Kyoto macaques. The authors show how 30 years of research (1979–2009) on this behaviour has elucidated the gradual transformation of stone-directed behavioural patterns that could be regarded as tool-use precursors and, as such, contributed to the understanding of cumulative culture in animals. They emphasise that Arashiyama is the first field site where a combination of longitudinal, comparative and experimental approaches has provided sound evidence for the long-term maintenance, inter-troop variability and social transmission of a single cultural behaviour in Japanese macaques. Finally, the authors argue that even traditional behaviours with no obvious function and no apparent adaptive value can not only be practised on a daily basis, and maintained over several decades within a social group, but can also be modified through the transgenerational accumulation of behavioural diversity and complexity.

In chapter 14, Shimada first provides a detailed structural analysis of 'social object play' (SOP) behaviour (i.e. social play while holding a portable object) in juvenile macaques at Arashiyama. He further explores a subcategory of SOP where multiple individuals treat a single object as the target of play and the object holder escapes from the others, referred to as 'play-chasing with a target

object' (PCT). He then goes on to compare SOP and PCT in the provisioned Arashiyama-Kyoto troop and the non-provisioned Kinkazan troop. His results show that PCT is an established play pattern in the former (where the objects held during play have a low nutritional value) but not in the latter (where the objects held are nutritionally valuable). To explain differences in PCT between the two troops, Shimada proposes a causal model about the effect of food condition on the dissemination of this particular play pattern. Finally, he discusses whether variation in the frequency and form of PCT between these two troops can be explained in terms of local traditions.

In their related essay, Pellis and Pellis (box 14.1) provide an overview on the form of play fighting across macaque species (e.g. number and age of participants, degree to which dominance and familial relationships influence the selection of play partners, and the type of attack and defence behavioural patterns). They argue that species differences in play relate to species differences in social systems and dominance styles, ranging from 'despotic' (e.g. Japanese macaques) to 'egalitarian' (e.g. Tonkean macaques). From this cross-species perspective, it is thus not surprising that in their play fighting, Japanese macaques tend to be more competitive, whereas Tonkean macaques tend to be more cooperative. Pellis and Pellis conclude by raising the question as to whether the mounting behaviour that pervades the play fighting of Japanese macaques is a by-product of the species' 'hyper-sexual' tendencies, or whether it is just an exaggeration of what occurs in other macaque species.

On a final note about play behaviour, Russon and Vasey (box 14.2) systematically compare the frequency, form and context of spontaneous eye-covering play (i.e. deliberately closing or covering one's eyes during a play sequence) in orangutans and in the colony of Arashiyama Japanese macaques housed at the Université de Montréal. Their findings suggest that eye-covering play in both Japanese macaques and orangutans does not involve pretending to be blind (i.e. acting as if one can't see, doesn't exist or exists in some altered form). However, it could involve relatively sophisticated cognition in the sense that actors may learn about the possibility of pretence by discovering the fallibility of mental representations when tested against the real world. The authors' observations demonstrate that Japanese macaques are more cognitively limited in their eye-covering play compared with orangutans, with only primary representations characterising the former, whereas secondary representations appeared to characterise the latter.

In chapter 15, Fujimoto explores the effects of the social style characteristic (i.e. strict dominance hierarchy and social asymmetry) on the form of grooming interactions among adult female Japanese macaques at Arashiyama. She does so by undertaking a systematic analysis of the behavioural sequences involved in adult female Japanese macaque allo-grooming episodes. Fujimoto

shows that the participants adopt different behavioural patterns depending on whether the grooming partner is kin or non-kin. She also points out that the participants change grooming roles in a symmetrical way. Finally, Fujimoto discusses such symmetrical role reversals in grooming in terms of the turn-taking occurring in human conversation.

In a related essay on grooming behaviour, Leca (box 15) reports the first case of dental flossing behaviour in Japanese macaques and considers its idiosyncratic presence in the Arashiyama-Kyoto troop as a grooming-related innovation. Since this behaviour is always associated with self- or allo-grooming activity, he suggests that the dental flossing innovation is a by-product of grooming. This tool-use innovation could be a transformation of grooming patterns via the running of hair between the teeth to remove louse eggs. He then proposes a possible scenario for the emergence of the different dental flossing techniques observed in the innovator. To explain why this behaviour has not yet spread to other group members, Leca discusses the various constraints on the social transmission of behavioural innovations within a group.

In chapter 16, Bélisle, Prud'homme and Dubuc experimentally analyse the influence of kinship degree, cost of resource defence by dominant individuals, and priority of access to the resource, on co-feeding in the Arashiyama Japanese macaques housed at the Université de Montréal. In their experimental approach, two adult females with a clear dominance relationship had access to a feeding box containing a limited amount of highly prized food. Their results show that kinship degree, defence cost and priority access all have a significant impact on co-feeding. In the first experiment they conducted, they found that the rates of tolerated co-feeding increased abruptly with degree of kinship, underscoring the importance of kin selection in the evolution of altruism in primates beyond the mother–offspring bond. In the second experiment they conducted, they showed that co-feeding time was significantly lowered when the costs of food defence for the dominant female were reduced, suggesting that a substantial proportion of the time spent in co-feeding during the first experiment may simply reflect a selfish strategy on the part of the dominant female not to expend energy, rather than altruism. In a third experiment, the authors demonstrate that when the subordinate female is given prior access at the feeding box, it substantially increases the co-feeding time of that female and her dominant counterpart. This result indicates that priority of access positively affects respect of possession from dominant females towards subordinate ones. In a final experiment, the authors demonstrate that the latter effect is even more prevalent in Tonkean macaques, a species with a more egalitarian system of dominance than that of Japanese macaques.

In chapter 17, Huffman and MacIntosh first provide a historical overview of the few studies on feeding ecology in Japanese macaques at Arashiyama.

They then combine information from records collected over a 45-year period to create the first comprehensive list, that has been published in English, of plant-foods consumed by the Arashiyama-Kyoto macaques. They point out that most of the previous reports were published in Japanese, and thus, have remained largely inaccessible to the larger primatological community. In order to determine the extent to which the Japanese macaques living at Arashiyama consume plant items that are potential medicinal foods, they compile an additional database listing those plant items containing secondary metabolites, as well as their potential role in health maintenance. Huffman and MacIntosh's impressive list aims to facilitate future work on this topic at Arashiyama and to stimulate similar work at other study sites across Japan. Such research may shed light on the major potential of plants for different forms of self-medication, including health maintenance, disease prevention and healing.

In the fourth and final section of the book, we provide two examples of the value of the Arashiyama macaques in terms of population management and public education. In chapter 18, Shimizu describes the effects of different administration methods and different doses of two types of hormonal contraceptives on the ovulatory cycles of female Japanese macaques living at Arashiyama. She shows that this hormone-induced sterility is reversible, since females eventually return to normal cycles and experience normal pregnancy after the treatment is stopped. Finally, Shimizu discusses the costs and benefits of various approaches for controlling fertility in Japanese macaque troops and how hormonal contraception could solve some of the current problems that are experienced between monkey parks and local human populations.

In the final chapter of our volume, Takenoshita and Maekawa (chapter 19) emphasise the major role of the Arashiyama-Kyoto macaques in science and environmental education in Japan. They point out that the Arashiyama site has a long history of collaboration between researchers, naturalists and educators in research and educational activities. After reviewing the current situation of science education in Japan, they discuss the positive role of the Iwatayama Monkey Park (Arashiyama Monkey Park in Japanese) as a field site for science education where primatologists have worked as collaborative educators. Finally, they introduce their own educational practices as an example of a contemporary attempt to form a new type of collaboration between educators and researchers. By regarding Arashiyama as a field site for education, Takenoshita and Maekawa show that the scientific value of Arashiyama macaques goes far beyond research.

Following the presentations of these research papers, our edited volume closes with a comprehensive bibliography of the scientific publications derived from 60

years of primatological research on the Arashiyama Japanese macaques (including the Arashiyama-Kyoto, Arashiyama West and Montréal troops). We hope this extensive (and impressive) listing will help readers in their search through the massive literature produced from work on the Arashiyama macaques, and stimulate further studies on this extraordinary monkey population.