

Sex Differences in Mortality of Japanese Macaques: Twenty-One Years of Data From the Arashiyama West Population

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ABSTRACT Theorists argue that mortality in male mammals should be higher than that of females, and many studies of primates followed across the life course have found this to be the case. This study examines mortality patterns in the rapidly expanding Arashiyama West (Texas) population of Japanese macaques (*Macaca fuscata*) and finds that males have a significantly lower median survival age (12.2 years) in comparison to females (20.5 years). Males and females are born in equal proportions, but by adulthood there are 2–5 females to every male. Males are at higher risk of falling victim to infectious diseases and human-related causes of death, and they are more likely to “disappear” from the population, which is inferred to result largely from emigration. There are no significant sex differences in the risks of dying from predation, non-infectious illnesses, neonatal defect, or social stress. Males become more susceptible to mortality than females once they reach sexual maturity, and they remain at greater risk than females until their old age. There is no evidence that one sex or the other is at greater risk of dying as infants, or as juveniles. Comparing males of different age classes, adolescent and adult males are more likely to die and to disappear than are juvenile males. These findings support the “high-risk, high-gain” hypothesis that males are mainly lost to the population because of their risk-taking behaviors after sexual maturity, rather than the “fragile male” hypothesis that males are more vulnerable to mortality during the period of growth and development. *Am J Phys Anthropol* 102:161–175, 1997 © 1997 Wiley-Liss, Inc.

Do male primates suffer higher mortality rates than females, and thus live shorter lives? A variety of theorists (e.g., Clutton-Brock et al., 1985; Daly and Wilson, 1978; Gadgil and Bossert, 1970; Ralls et al., 1980; Trivers, 1972, 1985) have argued that male mortality in mammals should be generally higher than that of females, and developed models to explain why. However, empirical data on primates have provided a variety of responses to this question, depending on which primate populations and which age classes are under consideration (e.g., see reviews in Dunbar, 1987; Hauser and Har-

court, 1992; Richard, 1981; van Schaik and de Visser, 1990).

Studies that have focused on the entire life course, rather than on one age category such as juveniles, have usually concluded that males have higher mortality rates overall and shorter life expectancies than females in a wide variety of primate species (e.g., Altmann and Altmann, 1970; Charles-Dominique, 1977; Cheney et al., 1988;

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Drickamer, 1974; Dunbar, 1980; Froehlich et al., 1981; Koford, 1966; Luder, 1993; Masui et al., 1975; Otis et al., 1981; Pope, 1968; Rajpurohit and Sommer, 1991; Robinson, 1988). Most demographic and life history studies of primates have found that while the two sexes are born in almost equal proportions, there are more females than males in the adult population. This apparent preponderance of adult females may be in part an artifact of field studies where the exact ages of individuals and locations of peripheral males are not known. Furthermore, a sexually-dimorphic growth pattern, in which males take longer than females to reach full body size, may lead observers to classify females and males of the same age as adults and subadults/juveniles, respectively. However, in some studies the exact birth dates, locations, and identification of all individuals are known, and there are still comparatively fewer males to females of given cohorts as one moves from younger to older age classes. This is true of Japanese macaques (*Macaca fuscata*), in which studies of known individuals tracked over their lifetimes have shown that the sex ratio at birth is approximately 1:1, but by adulthood there are nearly 5 females to every male (Sugiyama, 1976).

Lower male viability in mammals has generally been attributed to their greater risk-taking behaviors, such as emigration (most Old World Cercopithecoid species are male-dispersed, Pusey and Packer, 1987), and also to competition between males. In polygynous and polygamous species, agonistic encounters between males may render them more vulnerable than females to mortality, either through wounding or through the energetic costs of fighting when they could be foraging instead (Trivers, 1985). During migration between groups, male primates are frequently alone or in pairs and small groups, and they are ranging over unfamiliar areas, which renders them more susceptible to predators (Isbell et al., 1990; Richard, 1981). They also are exposed to a less predictable environment, especially in terms of resources, than are the females who remain in their natal ranges. Males attempting to enter new groups often encounter resistance from group members, especially

resident males, which may lead to serious wounding. A common assumption of primatologists is that it is during this crucial migration phase of life, usually corresponding to adolescence but sometimes occurring secondarily in adulthood, that males are most vulnerable to mortality (see overview in Richard, 1981). Rajpurohit and Sommer (1991), following Trivers (1985), refer to this as the "high-risk, high-gain strategy" of sexually mature males. A high-risk strategy may result in high mortality rates due to predation, agonism, and secondary infections during adolescence and adulthood. The high-gain part of the strategy is that the costs of dispersal for males may be offset by increased mating opportunities in their new ranges and groups as compared to their natal areas and groups.

Another hypothesis for lower male viability in mammals argues that in sexually dimorphic vertebrate species, juvenile males are more vulnerable than females to nutritional stress and starvation due to higher growth rates and lower levels of fat reserves in young males (e.g., Case, 1978; Clutton-Brock et al., 1985; Widdowson, 1976). van Schaik and de Visser (1990) refer to this idea as the "fragile male hypothesis" and it focuses on sex differences in juvenile, rather than adolescent/adult mortality (see also Debysier, 1995; Janson and van Schaik, 1993).

Our study addresses the question of differential mortality by sex over the life course in one population of Japanese monkeys, the Arashiyama West (AW) Texas group, and determines specific causes of death to which males are more vulnerable than females. Thus, we attempt to document what happens to males and females in the AW population in terms of mortality between the point of birth (when they exist in equal numbers) to the end of their lives, when adult females far outnumber the males. If males are lost to the population mainly due to the "fragile male hypothesis," then we predict differentially high male mortality during the juvenile phase. If males are lost to the population mainly due to the "high-risk, high-gain strategy," then we predict differentially heavy male mortality during the adolescent/adult phase.

METHODS

Study population

The Arashiyama population of Japanese monkeys was first found ranging near the outskirts of Kyoto, Japan, in 1954. At that time, Japanese primatologists counted a group size of 34 individuals and began to keep the detailed genealogical records which continue until the present. The population increased steadily from 1954 until 1966 when the 163-member group fissioned along female kinship lines into two daughter groups, subsequently named Arashiyama A and B. Both groups continued to expand until 1972, when 150 of the 158 members of Arashiyama A were moved to a ranch in south Texas and renamed the Arashiyama West (AW) group. These Japanese macaques were initially transferred to a 42.4-ha enclosure of native brushland, surrounded by an electrified fence, near Laredo, Texas, but in 1980 they were moved again to a 20-ha enclosure on ranchland near Dilley, Texas, 37 kilometers north of the first site. By 1980, there were approximately 300 monkeys in the group. In 1989, the Texas population fissioned into two groups, and by December 1993 (the end-point of this study), there were approximately 730 monkeys living in the two sister groups. For details of the history, demography, management, and environmental setting of the Arashiyama West population, see L.M. Fedigan (1991b), Huffman (1991), Koyama et al. (1992), and other references in Fedigan and Asquith (1991).

On both ranches in Texas, there have been mechanical problems with the electrified fence, such that males are able to emigrate, and the entire group sometimes ranges outside the enclosure. The monkeys are minimally provisioned and minimally disturbed by humans, and thus they forage on local flora and encounter local fauna. Once a day, food (monkey chow, grain, fruit) is spread from a truck along a road bisecting the enclosure and these provisions are usually completely consumed by the monkeys within the hour. Over the many years that the AW population has been located in south Texas, management and intervention practices have varied, however, only a few severely/terminally ill individuals have been removed from

the group for health reasons. In addition, between 1973 and 1987, 115 males and 86 females were trapped and sold to zoos to establish exhibits of Japanese macaques. These individuals are treated as "censored" observations in our analyses (see Data analyses below). Although the AW group is not living in its native habitat and is provisioned, several studies have shown that the demographic profile and life history pattern of these monkeys in Texas is similar to that observed for *M. fuscata* in Japan (e.g., Fedigan et al., 1983, 1986; Gouzoules et al., 1981, 1982; Koyama, 1980, 1984; Koyama et al., 1975, 1980; Masui et al., 1975; Sugiyama and Ohsawa, 1982; Wolfe, 1984a,b).

Under many field conditions it is difficult to determine exact causes and ages of death, whereas under caged conditions, the range of potential mortality factors is severely limited. A good compromise is a study population such as AW in which the monkeys are semi-free ranging and living in an environment that exposes individuals of known ages to a wide variety of causes of death, including predators (e.g., coyotes, bobcats, mountain lions, see Gouzoules et al., 1975), snake bites, infestations by parasites (e.g., Clark and Mano, 1975), poisonous plants (e.g., Joiner et al., 1975), infectious diseases (e.g., valley fever, L.M. Fedigan, 1991b; Pappagianis, 1983), and social stress (e.g., wounding by conspecifics, Fedigan, 1991b). Autopsies by veterinarians have indicated that these monkeys also fall victim to non-infectious ailments such as cancer, heart disease, osteoarthritis, and heat stroke. Although some specific causes of death are native to the south Texas environment, the general categories of mortality are applicable to primates everywhere.

Data collection

The AW population has been observed daily since its arrival in south Texas in February 1972, continuing the research regime that began in Japan in 1954. Censuses are conducted periodically, usually during the time period immediately following the provisioning of food. Individuals are noted as absent as soon as they fail to appear during the daily provisioning period. Once a monkey has been absent from feeding for

several days, it is recorded as having "disappeared." As noted by Sherman and Morton (1984), dispersal and mortality are notoriously difficult to separate in field studies because an animal's disappearance may be due to either emigration or to death. In the case of adolescent Japanese macaque males in Texas who are recorded as having disappeared, researchers are sometimes able to document that these monkeys have in fact emigrated or dispersed, because they are subsequently observed elsewhere on the large ranch. In the early years of this study, males who had left the group were trapped and sold to zoos when they were re-sighted. In more recent years, such males are trapped and held in south Texas in a smaller, "monkey-proof" enclosure.

Depending on which individual has been noted as absent, and depending on the human resources available at the time, a search may be made for the body of an individual that has disappeared. Bodies of dead monkeys are often found at the base of thick brush, into which they have crawled before dying. At other times, a body is found before the researchers have even noted the absence of an individual; this depends on the location of the cadaver, and how many people are regularly working within the monkey enclosure. If a body is found soon after death, or if a terminally ill individual is located, a veterinarian is asked to determine the cause of death. If the cadaver has been decaying for many hours, it is not possible to determine the cause of death, and the individual is recorded as having "died of unknown causes." At other times, the cause of death or injury is immediately apparent to the researchers, such as rattlesnake bites, electrocution, screwworm infestation, valley fever, or trauma from wounding during the mating season.

A wide range of mortality causes have been documented, and these were grouped into six larger categories for analysis: predation; infectious diseases and other environmental agents; non-infectious illnesses; neonatal defect/maternal neglect; social stress; and human-related causes of death (Table 1). In addition, some individuals have been lost to the population due to unknown causes (i.e., a body was found, but no cause was

TABLE 1. Causes of death for Japanese macaques in Arashiyama West, Texas (1972–1993)

Category of death	Causes of death
Predator related	Bobcat, mountain lion, coyote, dog, snake
Infectious diseases and other environmental agents	Pneumonia, flu, tetanus, viral encephalitis, valley fever, screwworm, coyotillo
Non-infectious illnesses	Cerebral palsy, osteoarthritis, lung embolism, heart and kidney dysfunction, stroke, heat stroke, gangrene, cancer, debilitation
Neonatal mortality	Neonatal defect/maternal neglect
Social stress	Orphaned, trauma, wounding by conspecifics, fighting/chases
Human related	Transfer, electrocution, euthanized, surgical complications, run over, exposed to cold weather
Unknown causes	
Disappeared	

determined), and some due to disappearances (i.e., no body was ever found). The category of neonatal defect/maternal neglect was recorded whenever an infant died within 4 months of birth from no obvious physical cause, but exhibited symptoms such as low weight, lethargy, and/or abandonment by the mother (death occurred in the first few days of life in 73% of these cases).

Genealogical records have been kept on each individual born into the group since 1954, beginning with their date of birth, sex, matrilineal history, matrilineal name (see L.M. Fedigan, 1991), tattoo number, mother's tattoo number, and nickname. When an individual is lost to the population, the date of death or disappearance is added to the individual's file, along with the cause of death, if known. The study sample for this paper consists of the deaths and disappearances recorded between 1972 and 1993; and the population entered into the survival analyses consists of all the monkeys ever recorded as living in Texas as determined from the cumulative genealogical records at the end of 1993.

Our study subjects were divided into the following age classes: infants (0–1 year), juveniles (1.1–4 years), adolescents (4.1–8 years), mature adults (8.1–15 years), and old adults (>15 years). Japanese macaque

males begin to produce sperm and females begin to cycle at 4.5 to 5 years, but full body size and, in males, full canine eruption, is not reached until approximately 8 years (Brizzee and Dunlop, 1986; Mori, 1979; Watts, 1985). In primates, the transition from immaturity to adulthood involves a multitude of variables that are interrelated, but not necessarily synchronous (Watts, 1990). Following Pereira (1993), juvenility in our study is considered to be that phase of the life course between weaning and sexual maturity. Adolescence, according to Watts (1985), is defined as the period of life beginning with sexual maturity and ending with the cessation of linear growth and attainment of full adult size. Old age in a Japanese macaque is more difficult to define for both sexes. Twenty years of age has been considered to be old age in female Japanese macaques (L. Fedigan, 1991; Nakamichi, 1991; Pavelka et al., 1991), but most males are dead by this age. Thus, 15 years was chosen as a value representing old age for both sexes.

Data analyses

The life table data were analyzed using the SPSS-PC program SURVIVAL, which makes use of both censored and uncensored intervals, and corrects for censoring. Analyses based only on completed (uncensored) lives is known to create a bias toward shorter intervals. Therefore, SPSS-SURVIVAL incorporates the analysis of both completed lives (data from dead animals), and the intervals that are incomplete or censored because the monkey had been sold to a zoo or was still alive at the end of the study. Survival analysis provides median survival time for male and female macaques, and performs a Wilcoxon-Gehan test to compare their survival distributions (Norušis, 1993a).

To examine whether sex affects the survival of our subjects, we ran a Cox regression model (also called the Cox proportional-hazards model; Dawson-Saunders and Trapp, 1994; Norušis, 1993a), with survival time as the dependent variable, and sex of the monkey as a co-variate. Cox proportional-hazards analyses provide a "relative risk" (RR) value based on the ratio of estimated hazard for a case *with* the characteristic, to

that for a case *without* the characteristic (i.e., males vs. females); this is a measure of the relative risk associated with the variable of being male. A relative risk greater than 1 indicates that the variable (being male) is associated with decreased survival. We ran Cox regressions for each group of mortality cases by comparing individuals that died from a particular cause (e.g., predation). Monkeys that died of other causes (e.g., all mortality cases except predation), live animals, and those that were sold, were treated as censored observations.

ANOVAS, regressions, Mann-Whitney U-Wilcoxon, Kruskal-Wallis, and High Log Linear tests were also run to answer questions about age and seasonal differences in death (Norušis, 1993b; Siegal and Castellan, 1988). The level of significance for all tests was set at $P < 0.05$.

RESULTS

Life tables

Six hundred and eighteen females (Table 2) and 612 males (Table 3) are recorded as having lived in the AW group in Texas between February 1972 (their arrival date) and December 1993 (the cut-off point for this study). One hundred and sixty-nine females and 185 males were lost to the population during this time period due to death or disappearance.

Overall, males in this population have a significantly lower median survival age (12.2 years), than do females (20.5 years; Wilcoxon-Gehan test, $W = 9.34$, d.f. = 1, $P < 0.001$). The longest recorded life span for a female AW macaque is 32 years ($n = 2$) and only 1.5% ($n = 9$) of females have lived beyond the age of 27. The longest recorded life span for a male in this group is 27 years ($n = 1$) and only 1.5% ($n = 9$) of the males have survived beyond the age of 20.

When the SURVIVAL analysis is repeated using only those individuals for whom cadavers were found (i.e., excluding disappearances), there is still a significantly lower median survival age for males (15.2 years) than for females (20.9 years; Wilcoxon-Gehan test, $W = 5.46$, d.f. = 1, $P = 0.019$). Thus, when cases of disappearance are excluded from the analysis, the median survival age of males increases by 3 years,

TABLE 2. Life table for female Japanese macaques¹

Age interval (in years)	Alive at beginning of interval	Censored (alive or sold)	Exposed to risk of dying	Died within interval
0-1	618	7	614.5	48
1-2	563	22	552.0	11
2-3	530	44	508.5	5
3-4	481	59	451.5	6
4-5	416	44	394.0	8
5-6	364	41	343.5	3
6-7	320	27	306.5	6
7-8	287	38	268.0	6
8-9	243	37	224.5	6
9-10	200	20	190.0	6
10-11	174	25	161.5	3
11-12	146	15	138.5	3
12-13	128	9	123.5	3
13-14	116	13	109.5	2
14-15	101	6	98.0	2
15-16	93	11	87.5	6
16-17	76	5	73.5	4
17-18	67	6	64.0	2
18-19	59	2	58.0	1
19-20	56	3	54.5	4
20-21	49	3	47.5	5
21-22	41	0	41.0	3
22-23	38	3	36.5	7
23-24	28	2	27.0	6
24-25	20	1	19.5	1
25-26	18	2	17.0	2
26-27	14	1	13.5	4
27-28	9	2	8.0	3
28-29	4	1	3.5	2
29-30	1	0	1.0	0
30-31	1	0	1.0	0
31-32	1	0	1.0	0
32-33	1	0	1.0	1
Total				169

¹ Median survival time = 20.7 years (248.9 months).

whereas the median survival of females remains the same.

As has been reported for this population in Japan (Koyama et al., 1992) most infant mortality in Texas occurs in the first 3 months of life. During the first year of life, infant mortality averages approximately 8.5% of births. There is not a significant sex difference in the mortality rates of infants or juveniles (see Sex ratios below), but as demonstrated by the life tables and by Figure 1, males begin to drop out of the population at a faster rate than females around the age of sexual maturity (4.5-5.0 years/54-60 months), and their survival rates are much lower than those of females throughout the rest of the life course.

Sex ratios

Male to female sex ratio at birth (1:1.01) is not significantly different from 1:1, and the

TABLE 3. Life table for male Japanese macaques¹

Age interval (in years)	Alive at beginning of interval	Censored (alive or sold)	Exposed to risk of dying	Died within interval
0-1	612	14	605.0	57
1-2	541	27	527.5	9
2-3	505	44	483.0	9
3-4	452	49	427.5	6
4-5	397	62	366.0	10
5-6	325	65	292.5	22
6-7	238	40	218.0	13
7-8	185	23	173.5	9
8-9	153	36	135.0	7
9-10	110	24	98.0	8
10-11	78	13	71.5	5
11-12	60	12	54.0	5
12-13	43	5	40.5	4
13-14	34	4	32.0	2
14-15	28	2	27.0	2
15-16	24	1	23.5	3
16-17	20	0	20.0	2
17-18	18	2	17.0	0
18-19	16	0	16.0	3
19-20	13	2	12.0	2
20-21	9	0	9.0	1
21-22	8	0	8.0	3
22-23	5	1	4.5	2
23-24	2	0	2.0	1
24-25	1	0	1.0	0
25-26	1	0	1.0	0
26-27	1	1	0.5	0
Total				185

¹ Median survival time = 12.2 years (145.9 months).

sex ratio stays close to 1:1 until the monkeys reach sexual maturity at age 5 (1:1.12), at which time males begin to decline in relative proportion to females (sex ratio at 10 years = 1:2.23; 15 years = 1:3.88; 20 years = 1:5.44). Although they are born in approximately equal numbers, by the time they are adults, the AW monkey population has about 2-5 females to every male.

Cause of death and survival time

There is a significant difference in the life expectancies at birth of monkeys that die from different causes (ANOVA including neonatal deaths: $F = 18.17$, d.f. = 7, $P < 0.001$; ANOVA excluding neonatal deaths: $F = 8.70$, d.f. = 6, $P < 0.001$). Monkeys that die of neonatal defect or maternal neglect, do so on average within 21 days of birth. Apart from neonates, monkeys that die of social stress have the shortest mean life expectancy (5.4 years) followed by those that die of predation (6.0 years). Individuals dying of human-related causes and those dying of infectious diseases have similar mean life expectancies

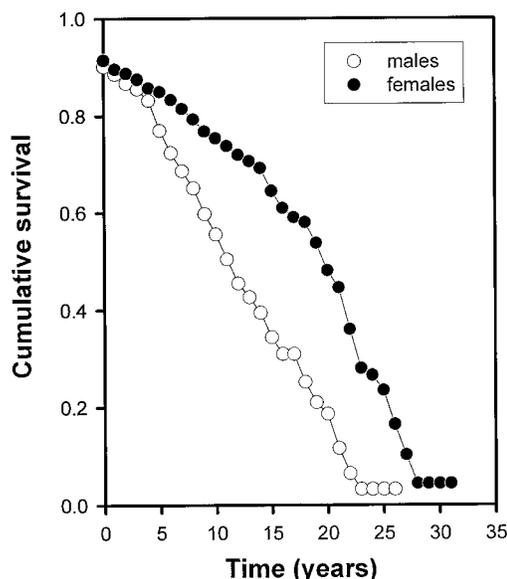


Fig. 1. Survival curves for male and female Japanese macaques (including all causes of death and disappearances).

(8.0 and 8.6 years, respectively), whereas those dying of non-infectious diseases live, on average, much longer lives (16.3 years). Monkeys that simply disappear from the population (which includes both dispersing males and deaths where bodies are not located) do so at a mean age of 7.2 years.

Sex differences in causes of death

There are sex differences in the proportions of monkeys dying of different causes, as well as monkeys dying of unknown causes, and those reported as having "disappeared" (Table 4). Of those females dying of known causes, the largest proportions died of neonatal defect/maternal neglect and non-infectious diseases. Of those males dying of known causes, the largest proportions died of neonatal defect/maternal neglect and infectious diseases.

The Cox regression tests were run for each category of mortality causes, as well as for disappearances and for the total sample of population losses, in order to compare the relative risk by sex. There was a significant difference in the *overall* relative risk of males compared to females; males have more

than twice the relative risk of being lost to the population as do females (Table 5). In terms of the 8 causes/categories of population loss, males are at significantly greater risk of falling victim to infectious diseases and human-related causes, and they are more likely to "disappear" (Fig. 2). There are no significant sex differences in risk of dying of the following causes: predation; non-infectious illnesses; neonatal defect/maternal neglect; social stress; and "unknown."

Age classes and death

In order to determine if more males than females are dying in different age classes (Table 4), Cox regressions were run comparing male and female risk of death within each of 5 age classes (infants, juveniles, adolescents, mature adults, and old adults) by combining all causes of mortality. There are no significant sex differences in the mortality of infants, or juveniles. However, males are at significantly greater risk than females of dying as adolescents, as mature adults, and as old adults (Table 5).

Since the two main hypotheses concerning sex differences in mortality postulate that male mammals are more likely to be lost from the population at one age than another, we also ran a Kruskal-Wallis test comparing the death/disappearance rates (number of animals that died and disappeared in each year of age/the number of individuals at the beginning of each year of age) of males in different age classes. There is a significant difference among the death/disappearance rates of juveniles, adolescents, mature and old adults (KW test, $\chi^2 = 11.85$, d.f. = 3, $P = 0.008$). We then ran Mann-Whitney U-Wilcoxon tests to determine which age categories differ from each other. There is a significant difference between the death/disappearance rates of juveniles and adolescent males (the latter exhibiting higher loss rates; $Z = -2.121$, two-tailed, $P = 0.034$) but not between adolescent and mature males ($Z = -1.604$, $P = 0.109$). The Mann-Whitney U-Wilcoxon tests were repeated following the exclusion of males that had disappeared, in order to ensure that we tested for age differences in mortality rather than emigration. The results are unaffected by

TABLE 4. Mortality cases by sex, age, and cause of death¹

	Entire population			Age									
				Infants		Juveniles		Adolescents		Mature		Old	
	F	M	Total [N (%)]	F	M	F	M	F	M	F	M	F	M
Starting cohort size	61	612		618	612	563	541	416	397	243	153	93	24
Cause of death													
Unknown	15	10	25 (7.1)	1	1	4	3	3	3	4	1	3	2
Predation	6	7	13 (3.7)	0	2	5	1	1	1	0	1	0	2
Infectious diseases	20	24	44 (12.4)	1	3	1	5	4	9	8	4	6	3
Non-infectious illnesses	25	12	37 (10.5)	0	0	0	2	0	5	4	2	21	3
Neonatal mortality	25	24	49 (13.8)	25	24	0	0	0	0	0	0	0	0
Social stress	8	3	11 (3.1)	3	0	1	0	3	3	0	0	1	0
Human-related	6	18	24 (6.8)	1	3	1	2	1	6	1	5	2	2
Disappeared	64	87	151 (42.7)	17	24	10	11	11	27	8	20	18	5
Overall (all causes)	169	185	354 (100.0)	48	57	22	24	23	54	25	33	51	17

¹ Age categories: Infants = 0–1 year; Juveniles = 1.1–4 years; Adolescents = 4.1–8 years; Mature = 8.5–15 years; and Old >15 years.

TABLE 5. Relative risk (RR) for males compared to females by cause of death and age¹

	RR	95% CI
Cause of death		
Unknown	1.14	0.49–2.62
Predation	1.74	0.55–5.48
Infectious diseases	2.22	1.19–4.10*
Non-infectious illnesses	1.84	0.88–3.86
Neonatal mortality	0.97	0.56–1.70
Social stress	0.48	0.12–1.87
Human related	6.78	2.40–19.1**
Disappeared	2.38	1.68–3.35**
Overall (all causes)	2.21	1.53–2.38**
Age		
Infants (0–1 year)	1.22	0.84–1.78
Juveniles (1.1–4 years)	1.20	0.67–2.17
Adolescents (4.1–8 years)	2.98	1.82–4.78**
Mature (8.1–15 years)	3.07	1.83–5.17**
Old (>15 years)	2.24	1.23–3.98**

¹ Relative risk (RR) based on Cox regression. CI, confidence interval.

* $P < 0.01$.

** $P < 0.001$.

the exclusion of such males; the death rates of juveniles and adolescents are still significantly different, with adolescents exhibiting higher death rates ($Z = -2.121$, $P = 0.034$), and the death rates of adolescent and mature males are still not significantly different from each other ($Z = 0.00$, $P = 1.000$).

Seasonal timing of deaths

To clarify the reasons for sex differences in mortality, we also examined seasonal effects on mortality rates. If males are dying mainly due to the effects of male competition, then we would expect higher rates of male mortality during the mating season than the other half of the year. If males are dropping out of

the population mainly due to the stresses of emigration, then we would expect higher male mortality rates during the birth season when male Japanese macaques are more prone to leave the social group (Koyama et al., unpublished data; Sugiyama, 1976). If females are more vulnerable to mortality causes when they are stressed by male aggression during the mating season, then we would expect higher rates of female mortality during the mating season. However, if females are more stressed by the reproductive costs of gestation, lactation, and parturition, or by female-female competition, then we would expect higher rates of female mortality during the birth season (Jolly, 1984).

Mortality dates were divided into two halves of the year: March to August, corresponding to the birth season; and September to February, corresponding to the mating season. Because neonatal deaths occur by definition in the birth season, they were removed from all analyses of seasonality. Disappearances were analyzed separately from known deaths in which cadavers were found. Neither males nor females are more likely to die (cadavers found) during the birth season than the mating season (Males: $\chi^2 = 0.02$, $n = 63$, d.f. = 1, $P = 0.899$; Females: $\chi^2 = 1.35$, $n = 74$, d.f. = 1, $P = 0.245$). However, both males and females are significantly more likely to disappear during the birth season (Males: $\chi^2 = 17.285$, $n = 63$, d.f. = 1, $P < 0.001$; Females: $\chi^2 = 10.52$,

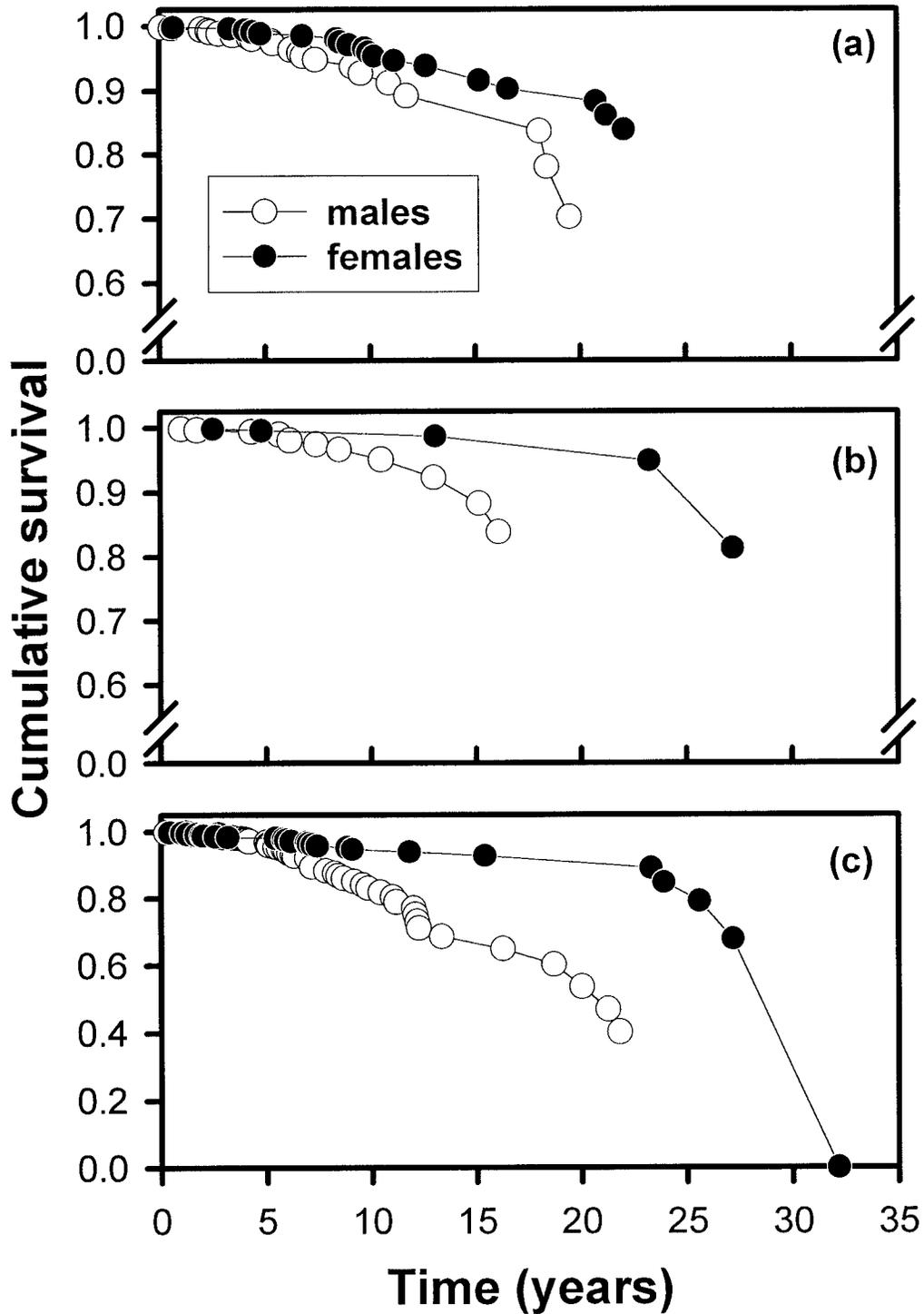


Fig. 2. Survival curves for male and female Japanese macaques lost to the population due to: (a) infectious diseases; (b) human-related causes; and (c) disappearances. Note: the range for the Y-axis for c extends

from 0.0 to 1.0 whereas for a and b it extends from 0.5 to 1.0, because the cumulative survival for macaques which disappeared (c) is less than the that for infectious diseases (a) or human-related (b) mortality.

$n = 46$, d.f. = 1, $P = 0.001$). In fact, there have been approximately three times as many disappearances overall in the birth season as in the mating season. Life history data from the Arashiyama population prior to translocation (1954–71) show that males in Japan were also more likely to disappear during the birth rather than the mating season ($n = 73$, $\chi^2 = 5.170$, d.f. = 1, $P = 0.023$), but no cases of female disappearance were recorded in Japan.

A confounding factor in any seasonal analysis is that mean monthly temperatures in the very hot climate of south Texas rise steadily from January through August (largely corresponding to the birth season), and then begin to decline from September to December (approximating the mating season). Weather data were obtained from the National Climatic Data (NCD) Center, whose records include tri-monthly recordings of max-min temperatures at both the Laredo and Dilley sites in each month since February 1972. A multiple regression of NCD Center weather data demonstrated a positive relationship between the rate of deaths and disappearances in a given month and the highest temperature recorded for that month ($R^2 = 0.13$, $F_{1, 122} = 32.38$, $P < 0.001$). However, our calculations also showed that between 1972 and 1993, 75% of the months with maximum temperatures $>30.5^\circ\text{C}$ occurred during the birth season, and 74% of the months with maximum temperatures below the median of 30.5°C occurred during the mating season. Thus, the birth season in Texas consists almost entirely of “hot” months, and the mating season occurs during cooler months, rendering it infeasible to disentangle the effects of seasonal behaviors (emigration, agonism, reproduction) from the possible effects of heat stress on mortality in the AW population.

Rainfall in Texas is sparse and largely erratic, but the rainiest months are in May and September. We did not find a significant relationship between mean monthly precipitation and the number of deaths and disappearances in that month for males ($r^2 = 0.201$, d.f. = 11, $P = 0.143$) or for females ($r^2 = 0.154$, d.f. = 11, $P = 0.21$).

DISCUSSION

Do males in the Arashiyama West population have shorter life expectancies than females?

Males in the study population have a significantly lower survivorship than that of females. Although ages of death and hazard rates are not published for Arashiyama monkeys in Japan, the sex ratios and life table data published on other provisioned populations of macaques in Japan indicate that the same life history pattern occurs in their native habitat (e.g., Masui et al., 1975; Sugiyama, 1976). Also, overviews of mortality in mammals suggest that heavier male mortality is common in female-philopatric, male-dispersed species (e.g., Clutton-Brock et al., 1982; Daly and Wilson, 1978; Ralls et al., 1980; Trivers, 1985).

What causes the deaths of males and females?

In this population, the most common cause of death is neonatal defect/maternal neglect. Other frequently occurring mortality causes are infectious diseases and non-infectious illnesses. Predation, social stress (including wounding), and human-related deaths are far less common. Males and females are not at different risk of neonatal deaths, predation, non-infectious illness, or social stress.

Males are significantly more likely than females to die from infectious diseases and human-related causes. Males are also significantly more likely to simply “disappear” from the population than are females, and since solitary males are sometimes spotted and trapped elsewhere on the ranch, we infer that many of these males have emigrated. The finding that more males than females die of human-related causes, such as being electrocuted on high tension wires, or being run over by vehicles, is probably also related to emigration, since most of these deaths occur when the monkey is traveling outside the enclosure.

The category of infectious diseases is called “infectious diseases and other environmental causes” because it includes parasitic infestation and death from ingesting poisonous berries (“coyotillo”), although most deaths in this category are brought about by actual

infections such as pneumonia and valley fever. There is some evidence that male mammals are more vulnerable to disease (Ralls et al., 1980; Trivers, 1985). Androgens have a suppressive effect on both humoral and cell-mediated immunity which may result in greater susceptibility of male mammals to parasitic infections and other infectious diseases (e.g., Alexander and Stimson, 1988).

At what age(s) are males more likely to die?

Males become more susceptible to mortality than females once they reach sexual maturity at approximately 4.5 years of age, and they remain at greater risk until their old age. There is no evidence in this population that either males or females are at greater risk of dying when they are infants, or when they are juveniles.

A recent article by van Schaik and de Visser (1990), as well as Dittus's earlier papers on toque macaque demography (Dittus, 1977, 1980) focused on juvenile mortality in primates, and concluded that when food is limited, females are the less viable sex in this age-class. Dittus argued that juvenile female macaques are subordinate to males and thus, under non-provisioned conditions, have less access to resources (food, water, refuges) and lowered viability. van Schaik and de Visser (1990) compared 40 data sets from different primate populations, and also concluded that mortality among juveniles in female-bonded species is female-biased when food is limited, whereas no sex difference is observed when access to food is unlimited. They attributed higher juvenile female mortality largely to harassment of juvenile females by unrelated adult females (see also Rhine et al., 1988). Hauser and Harcourt (1992) critiqued van Schaik and de Visser's paper on the basis of sampling error and reanalyzed their data, coming to different conclusions, one of which is that in provisioned macaque groups, there may be a slight bias to heavier juvenile *male* mortality (see rejoinder in van Schaik, 1992). As described in Methods, the AW population is minimally provisioned once a day, and provisioned foods can be best described as abundant, but not "unlimited," since the

chow and grain is consumed within the hour, and the monkeys spend most of each day foraging on local vegetation. Our findings support the conclusion of Ralls et al. (1980) that juvenile mortality rates are similar in male and female mammals when food is abundant.

Comparing mortality across males of different age classes, we found that adolescents and mature adults have significantly higher rates of death from known causes than do juvenile males. Adolescent and mature males are also far more likely to "disappear" from the population than are juveniles. Thus, we can localize the vulnerable phase of the life course for males in this study population as occurring after sexual maturity.

What processes underlie the observed mortality patterns?

Mortality causes can be roughly categorized into extrinsic (i.e., environmental) vs. intrinsic (i.e., growth, biological aging) factors. Luder (1993) argues that extrinsic causes of death in macaques are most common in the middle phase of life. According to Luder, in the earliest phase of life young monkeys are more prone to die of birth defects, starvation, and general "unfitness for life," and in the last phase old monkeys are likely to die of senescence or degenerative disease, but in the prime of life, environmental causes of death prevail. Similarly, we found that different causes of death are associated with certain ages: birth defects and maternal neglect lead to many deaths in the first year of life, monkeys that perish of social stress and predation die young, those dying of human-related causes and infectious diseases are middle aged, and those dying of non-infectious disease live on average much longer lives. We also found that AW monkeys of both sexes are equally likely to die as infants and juveniles, and as adults, both sexes are equally likely to die of non-infectious illness, which include several degenerative ailments such as osteoarthritis and cancer. Like Luder, we found that environmental causes of death mainly strike the middle-aged monkey, and furthermore, we found that sexually mature males are more likely than females to die of extrinsic, environmental causes.

How much of male mortality during adolescence and adulthood is due to the stresses of attempted emigration, and how much is due to male-male competition? It is not possible to answer this question directly with our data set, nor would all the stresses of emigration and competition have a direct impact on mortality in any case. There are only a few cases in the AW records of death from social stress (i.e., fighting, chasing, and wounding), but individuals who have lost agonistic encounters may be rendered more vulnerable to other mortality agents (see Sapolski, 1984, 1994), and thus may not be recorded as having died directly from social stress. For example, Rawlins and Kessler (1982) found that deaths of Cayo Santiago rhesus macaques from tetanus peak during the mating season when aggression leads to wounding and subsequent infection (see also Vandenbergh and Vessey, 1968; Wilson and Boelkins, 1970). One method of addressing this issue inferentially is to determine whether male mortality is more common during the mating season when males are more likely to be engaged in agonistic encounters, or during the birth season, when males are more likely to leave the group. A seasonal analysis of mortality also addresses inferentially the question of whether females are more stressed by the aggression that they receive from males during the mating season, or by the reproductive and social costs of female-female competition during the birth season.

Strictly in terms of bodies found, neither males nor females are significantly more likely to die during the birth or the mating season, suggesting that agonism, emigration, and reproductive activities may all be commensurably costly. Both males and females disappear more often during the birth season. Unfortunately, this finding is confounded by the fact that the birth season corresponds almost entirely to the months when mean maximum temperatures in south Texas rise above 30.5°C. Heat stroke has only been recorded as the cause of death in 4 cases, but very high temperatures during the birth season could conceivably create stress that renders monkeys more vulnerable to other factors. Given the evidence, however, that known deaths (bodies found)

are *not* more common in the birth season and that the same seasonal pattern of male disappearances occurs in Arashiyama, Japan, where excessively high temperatures are uncommon, we think it unlikely that heat stress is responsible for the greater rate of disappearances during the birth season. It is seldom possible to accurately separate mortality from emigration when animals disappear from their population (Caughley, 1966, 1977). But the Japan data and the more frequent sightings of male monkeys elsewhere on the Texas ranch during the birth season, suggest that attempted emigration, more than heat stress or male-male agonism, is the underlying factor driving the relationship we found between reproductive seasons and male disappearances.

In the 21 years of this study, only one elderly female has been confirmed to leave the group, so attempted emigration cannot explain our finding that more females also disappear during the birth season. However, females do temporarily move away from the group to a secluded area to give birth, and if they die during parturition, it is likely that their bodies would not be found and they would be recorded as having disappeared. Thus, reproductive costs may be an important factor in female disappearances during the birth season. We suggest that although both males and females are more likely to disappear during the birth season, the underlying factors in this pattern of population loss may be different for the two sexes.

In our study, infant males and females are not significantly different in mortality patterns, nor are juvenile females more likely to die than males. Sex differences in mortality begin to appear in the adolescent stage and continue through adulthood into old age, leading to a significantly lower life expectancy for male Japanese macaques. Males are at greater risk than females of disappearing and of dying from infectious diseases and human-related causes. Many of these male disappearances are inferred to result from attempted emigration. These conclusions lend support to the hypothesis that males are mainly lost to the population through a high-risk, high-gain strategy followed during the adolescent and adult stages, rather than because males are more

fragile than females during the period of growth and development. Although it is not possible to elucidate all aspects of sex-differentiated mortality in the AW population, the results of this study begin to clarify how and when males and females are lost to the population between the point of birth, when they exist in equal proportions, and the end of their lives, when females far outnumber males.

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