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ORIGINAL ARTICLE

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Birth-season variation in Japanese macaques, *Macaca fuscata*

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Abstract Japanese macaques, *Macaca fuscata*, exhibit an annual reproductive cycle that apparently is maintained intrinsically. Translocation of nine troops to new latitudes within the northern hemisphere has had minimal effect on the timing of birth seasonality in these troops; translocation of one troop to the southern hemisphere has resulted in a 6-month forward displacement of birth seasonality in this troop. Limited available evidence indicates that, in the latitudinal zone between Toimisaki (31°22′N) and Kinkazan (38°17′N), mean birth date in in-situ troops becomes earlier as latitude of troop localities increases; the same relationship between mean birth date and latitude apparently does not apply to in-situ troops south and north of the Toimisaki–Kinkazan latitudinal zone. Within the Toimisaki–Kinkazan latitudinal zone, earlier mean birth dates at higher latitudes may permit infants to achieve an adequate level of development before the earlier onset of poor winter food conditions. South of the Toimisaki–Kinkazan latitudinal zone, winters are relatively mild and may be less of a factor in infant survival; north of this zone, poor winter food conditions persist so long that earlier infant births may be maladaptive.

Keywords Birth seasonality · Japanese macaques · Latitudinal variation · *Macaca fuscata* · Translocation

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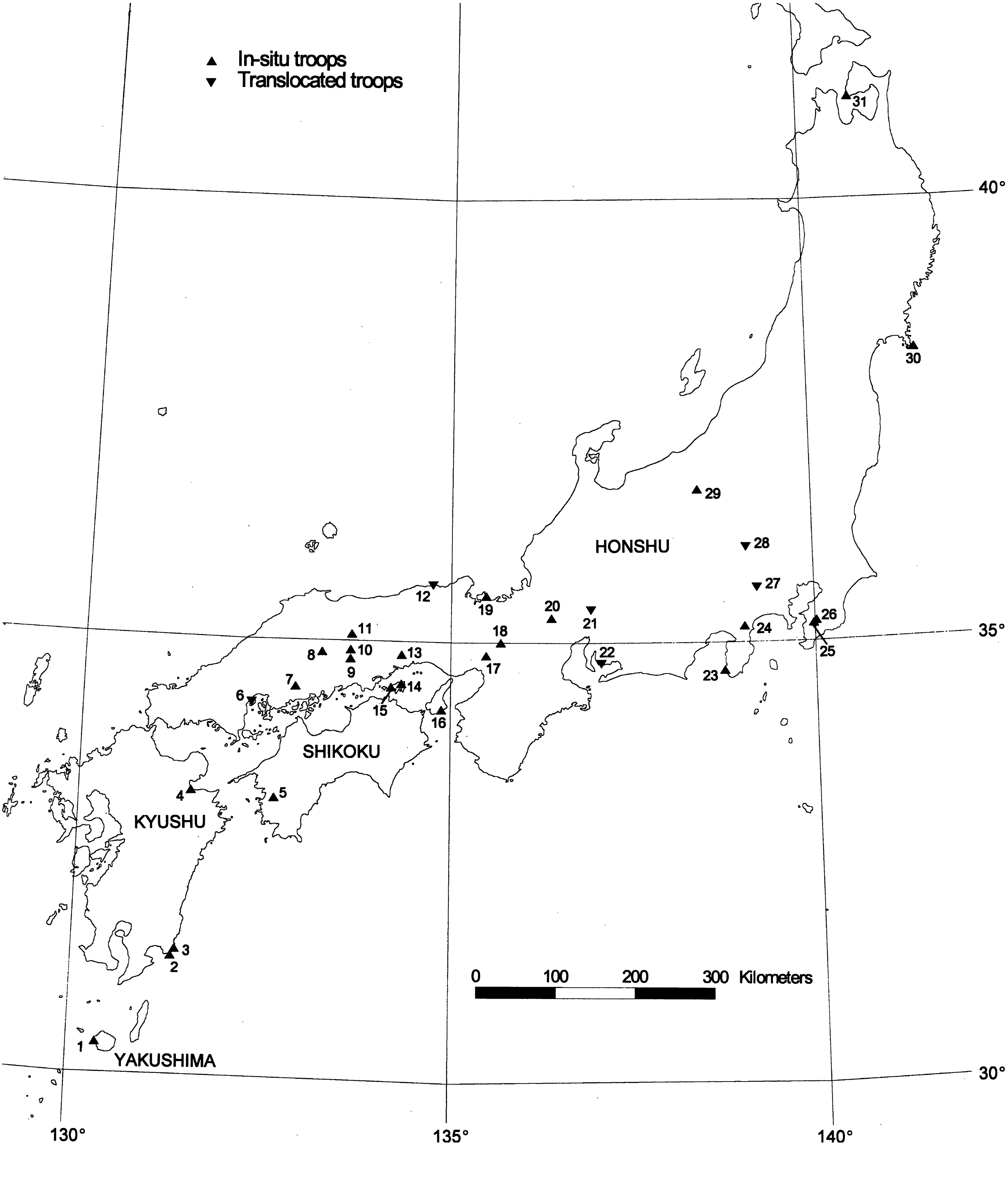
Introduction

Matings in Japanese macaques, *Macaca fuscata*, normally occur during the autumn and winter (September–February) and, following a gestation period of about 173 days, births normally occur during the spring and summer (March–August; Kawai et al. 1967, p. 40; Nozaki et al. 1992, p. 301). Birth seasonality obviously is a direct consequence of mating seasonality (cf. Takahashi 2002, p. 145). However, because field data concerning birth seasonality are much more abundant than those concerning mating seasonality, the present study of variation in reproductive seasonality in *M. fuscata* focuses on birth seasonality. Available evidence, including old and new information, concerning the nature and causes of birth-season variation in this species is suggestive but not conclusive.

Birth seasonality in in-situ troops in Japan

The seminal article on geographic variation of birth seasonality in *M. fuscata* was published by Kawai et al. (1967, p. 38). These authors studied birth-season dates in 25 troops of this species (Fig. 1; Table 1; Appendix 1); nineteen of these (including two with incomplete data) were natural troops observed in native habitats, five were natural troops that had been transported to new localities, and one was an artificial group composed of individuals captured on Yakushima and transported to Honshu. Concentrating attention on in-situ natural troops with complete data, Kawai et al. (1967, p. 44) noted a general tendency for birth seasons at northern latitudes in Japan to occur earlier than those at southern latitudes (cf. Lancaster and Lee 1965, p. 498); as exceptions, birth seasons on Shodoshima and at Funakoshiyama appeared to be earlier than expected, relative to the latitude of these localities (Kawai et al. 1967, p. 43; cf. Fig. 2; Appendix 1).



The data of Kawai et al. were reexamined by Van Horn (1980, p. 192) and Fedigan and Griffin (1996, p. 377). The authors of each of these studies selected data for 11 of Kawai et al.'s troops (10 troops in common to both studies) and confirmed the correlation between latitude and birth-season dates.

Cozzolino et al. (1992, p. 332) also reexamined the data of Kawai et al., including both in-situ and translocated troops in their analysis. These authors found a positive correlation between temperature at nearby weather stations and mean birth date in 25 troops [including two translocated troops not studied by Kawai

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Fig. 1 Distribution in Japan of *Macaca fuscata* troops for which birth seasonality data are available. *In-situ troops* (see Appendix 1). *Latitude 31–37*°N (localities studied by Kawai et al. 1967, pp. 38–39): *2* Toimisaki; *3* Kojima; *4* Takasakiyama; *5* Nametoko; *7* Kochi; *8* Taishakukyo; *9* Gagyusan; *10* Kanbanotaki; *13* Funakoshiyama; *14* Rosando; *15* Choshikei; *17* Minoo-A; *18* Arashiyama; *23* Hagachi; *25* Takagoyama-S; *26* Takagoyama-A; *29* Jigokudani. *Latitude* <*31*°N or >37°N: *1* Nina-A; *30* Kinkazan A; *31* Wakinosawa. *Supplementary localities*: *11* Katsuyama; *16* Kaminada. *19* Otoumi; *20* Ryozen-A; *24* Hakone. *Translocated troops* (see Table 1): *6* Miyajima; *12* Takeno; *21* Ohirayama; *22* Okinoshima; *27* Takaosan; *28* Hodosan

et al. (1967, p. 38)]; it should be noted that local temperature generally decreases as latitude increases (cf. Hamada et al. 1996, p. 99).

All of the above analyses of geographic variation in birth seasonality in in-situ *M. fuscata* troops are restricted to localities north of 31°N and south of 37°N, which excludes the southernmost and northernmost extremes of the species range (ca. 30°15′–41°30′N; Fig. 1). Data are now available for troops at three localities outside of the 31–37°N latitudinal zone (Nina-A, Yakushima, 30°21′N; Kinkazan A, 38°17′N; and Wakinosawa, Shimokita Hanto [Peninsula], 41°08′N) and for five supplementary localities within the 31–37°N latitudinal zone (Appendix 1).

Of troops at the three localities outside of the 31–37°N latitudinal zone, the mean birth date of one–Kinkazan A–fits well on the birth-date/latitude regression line determined by mean birth dates of the 17 in-situ troops with complete data that were studied by Kawai et al. (1967, pp. 38–39; Fig. 2). For these 18 troops, from Toimisaki (31°22′N) in the south to Kinkazan A (38°17′N) in the north, the negative regression between latitude and mean birth date ($r = -0.764$, $P < 0.01$) slightly exceeds that for Kawai et al.'s 17 troops, excluding Kinkazan A ($r = -0.737$, $P < 0.01$). At 31°N on the Toimisaki–Kinkazan regression line, the predicted mean birth date is 30 June; at 38°N, the predicted mean birth date is 20 April, more than 2 months earlier than at 31°N.

Available evidence for troops at the remaining two localities outside of the 31–37°N latitudinal zone (Nina-A, Yakushima; Wakinosawa, Shimokita Hanto) indicates that birth seasonality in these troops does not conform to the Toimisaki–Kinkazan regression (Fig. 2); the regression that aggregates Nina-A and Wakinosawa with the 18 Toimisaki–Kinkazan localities is not significant ($r = -0.441$, $P > 0.05$), unlike the regression that excludes Nina-A and Wakinosawa (see above). South of 31°N, in the Nina-A troop (30°21′N), the mean birth date (30 April) apparently is approximately 2 months earlier than–not, as predicted, later than–the mean birth dates (30 June and 2 July, respectively) at Toimisaki and on Kojima (ca. 31°30′N); the mean birth date is similarly early (12 May) in the Yakushima population that was translocated to Ohirayama, Honshu (Table 1). Suzuki et al. (1998, p. 318) have previously noted that the birth season on Yakushima, at the southern limit of distribution of *M. fuscata*, occurs during approximately the same months as the birth season on Kinkazan, which is nearly 8° north of Yakushima and only approximately 3° south of the northern limit of distribution of the species.

North of 37°N, at Wakinosawa (41°08′N), the mean birth date (13 May) is slightly later than–not, as predicted, about 35 days earlier than–the mean birth date (26 April) on Kinkazan (38°17′N; Fig. 2). The apparently anomalous timing of the birth season on Shimokita Hanto was previously suggested by Kawai et al. (1967, p. 42). Information concerning earliest and latest birth dates (mean birth dates unknown) for troops at five supplementary localities within the 31–37°N latitudinal zone (Appendix 1) suggests that birth seasonality in these troops conforms reasonably well with the Toimisaki–Kinkazan regression (cf. Fig. 2).

Birth seasonality in translocated troops

Data concerning birth seasonality are available for ten translocated troops–six translocated within Japan, three translocated from Japan to northern hemisphere localities in the United States or Italy, and one translocated from Japan to Tasmania, in the southern hemisphere (Table 1; Appendix 2). Birth seasonality in troops translocated across up to 11° of latitude (Mihara/Beaverton) to northern hemisphere localities in Japan, North America, and Europe is generally similar to that in corresponding in-situ troops in Japan, as noted by previous authors (Kawai et al. 1967, p. 47; Cozzolino et al. 1992, p. 329; Nozaki et al. 1992, p. 308; Nozaki 1993, p. j97; Fedigan and Griffin 1996, p. 374). In contrast, translocation of a troop across about 80° of latitude, from the northern hemisphere to the southern hemisphere (Kasuga/Launceston), has resulted, within 18 months, in forward displacement of the birth season by approximately 6 months.

Long-term birth-season variation in a translocated population

Birth records of a *M. fuscata* population translocated from Yakushima to Honshu have been carefully maintained for 45 years by the Japan Monkey Centre (Fig. 3; Appendix 2). The progenitors of this population were 81 monkeys captured at various unrecorded localities on Yakushima (ca. 30°20′N) and released at Ohirayama (35°23′N), Honshu, in March 1957 (Kawai 1960, pp. 204, 222). The population was permitted to range freely, with minimal provisioning, at Ohirayama until August 1986, when, as a result of complaints by local residents, the monkeys were recaptured, confined to a fenced enclosure at the site, and fed pellets; to control population growth, some of the female monkeys were given contraceptive pills, and the most prolific females were

Table 1 Birth seasonality comparisons of in-situ and translocated troops of *Macaca fuscata*

Troop	Locality	Island	Latitude (N)	Longitude (E)	Earliest birth	Latest birth	Mean birth	No. births	Observation years	References[a]
Yakushima/Ohirayama translocation (to Ohirayama, 1957; to nearby Japan Monkey Centre, 1997)										
In situ	Nina-A	Yakushima	30°21′	130°23′	14 March	early July	30 April[b]	> 22	1976–1978, 1997–1998, 2000–2002	1
Translocated	Ohirayama[c]	Honshu	35°23′	136°56′	15 February	3 October[d]	12 May[e]	458	1957–1986	2
Shodoshima/Okinoshima; Miyajima; Takaosan translocations										
In situ	Choshikei	Shodoshima	34°29′	134°11′	March	June	24 April	149	1958, 1960–1962, 1966	3
In situ	Rosando	Shodoshima	34°31′	134°19′	March	June	10 May	80	1958–1960, 1962	3
Translocated		Okinoshima	34°46′	137°04′	March	June	18 April	57	1958–1966	3
Translocated		Miyajima	34°17′	132°18′	March	June	4 April	51	1962–1966	3
Translocated	Takaosan	Honshu	35°37′	139°13′	March	July	3 May	62	1958–1966	3
Kochi/Takeno translocation										
In situ	Kochi	Honshu	34°28′	132°53′	April	July	7 June	24	1958–1959	3
Translocated	Takeno	Honshu	35°39′	134°45′	April	June	14 May	25	1965–1966	3
Gagyusan/Hodosan translocation										
In situ	Gagyusan	Honshu	34°48′	133°37′	April	August	27 May	243	1956–1966	3
Translocated	Hodosan	Honshu	36°05′	139°05′	April	August	29 May	61	1963–1966	3
Takasakiyama/Rome translocation										
In situ	Takasakiyama	Kyushu	33°14′	131°31′	April	October	3 July	1,067	1958–1966	3
Translocated	Rome	(Italy)	41°56′	12°30′	May[f]	September[g]	17 July	109	1977–1989	4
Mihara (near Kochi)/Beaverton translocation										
In situ	Kochi	Honshu	34°28′	132°53′	April	July	7 June	24	1958–1959	3
Translocated	Beaverton	(U.S.A.)	45°29′	122°48′W	March	August	27 May		1965–1980	5
Arashiyama/South Texas translocation										
In situ	Arashiyama	Honshu	35°00′	135°41′	late March	early September	28 May	416	1957–1971	6
Translocated	SouthTexas	(U.S.A.)	28°05′	99°15′W	mid March	early September	23 May	795	1974–1976, 1978–1989	6
Kasuga/Launceston translocation										
In situ	Kasuga	Honshu	35°10′	135°09′	March	August				7
Translocated	Launceston	(Tasmania)	41°35′S	147°22′	6 November[h]	11 December	19 November	4	1980–1982[i]	7

[a] Key to references: 1 Appendix 1; 2 Appendix 2; cf. Kawai et al. 1967, p. 38; 3 Kawai et al. 1967, p. 38; 4 Cozzolino et al. 1992, p. 331; cf. Cozzolino and Schino 1998, p. 860; 5 Van Horn 1980, p. 198; Rostal et al. 1986, p. 453; 6 Fedigan and Griffin 1996, p. 375; 7 Nozaki et al. 1992, pp. 302, 308; Nozaki 1993, p. j97

[b] SD = 25.8 days

[c] Free-ranging period only

[d] Includes three unusually late births (19 September 1959, 29 September 1968, and 3 October 1965); excluding these three births, the latest birth date recorded for this population during the free-ranging period is 10 August

[e] SD = 31.7 days

[f] Excludesone aberrant birth in March

[g] Excludes two aberrant births in November

[h] Excludes one transitional infant born 14 March 1981, apparently conceived according to the northern hemisphere schedule; the next infant produced by this mother was born 15 November 1982, apparently conceived according to the southern hemisphere schedule

[i] Quarantined in Melbourne June–September 1980; released in corral in Launceston 20 September 1980

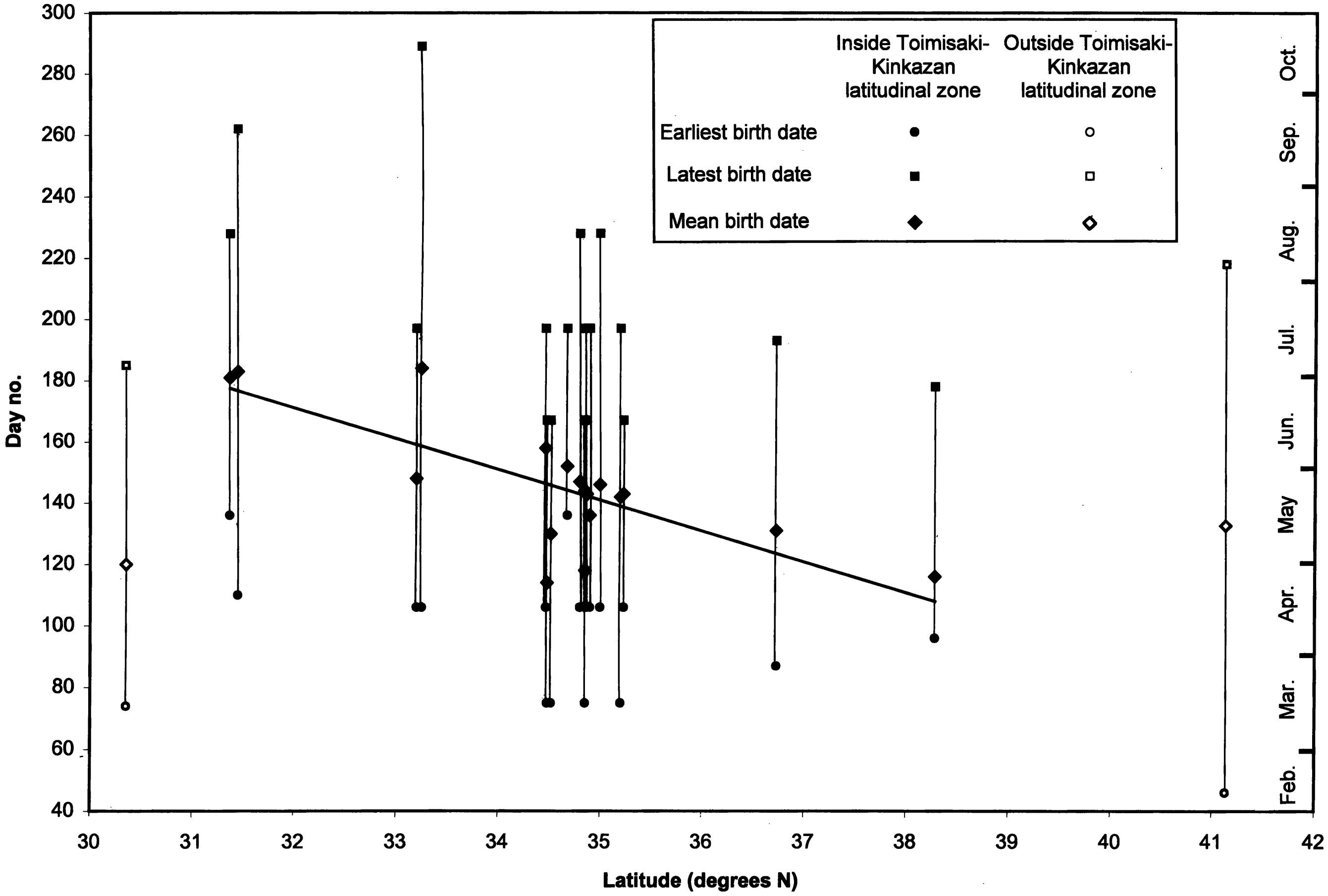

Fig. 2 Latitudinal variation in birth seasonality in in-situ troops of *M. fuscata*. Seasonality in 18 troops distributed within the Toimisaki–Kinkazan latitudinal zone (31°22′–38°17′N) is compared with seasonality in troops on Yakushima (Nina-A, 30°21′N) and Shimokita Hanto (Wakinosawa, 41°08′N); for documentation, see Appendix 1. (Regression equation, $y = -10.07x + 493.4$; $r = -0.764$, $F = 16$, $P < 0.01$)

removed from the group (A. Katoh, Japan Monkey Centre, personal communication). Finally, in 1997, the population was moved from the enclosure at Ohirayama to an enclosure at the nearby Japan Monkey Centre.

From 1957 through 1986, when the population ranged freely at Ohirayama, the 30-year mean birth date was 12 May (Fig. 3; Appendix 2), which, as previously noted (Table 1), is close to the mean birth date of an in-situ troop on Yakushima (30 April); during these 30 years, the annual mean birth date fluctuated between 19 April and 16 June, but these fluctuations did not trend either earlier or later (regression, $y = 0.1529x - 167.6$; $r = 0.109$; $F = 28$; $P > 0.05$). From 1987 through 2001, when the population was confined to enclosures at Ohirayama and the Japan Monkey Centre, the 15-year mean birth date was 3 May, the annual mean birth date fluctuated between 16 April and 22 May, and the annual mean birth date tended weakly to become slightly earlier (regression, $y = -1.134x + 2384$; $r = -0.519$; $F = 13$; $0.05 > P > 0.01$). The birth seasonality of this population apparently was not affected by its translocation to an unconfined habitat (1957–1986), but it may have been affected by conditions of the population's subsequent confinement (1987–2001).

Laboratory studies of birth seasonality

Nozaki and colleagues have conducted an important series of laboratory studies of birth seasonality in *M. fuscata* (Nozaki 1991, p. 104; Nozaki et al. 1992, pp. 302, 313). These authors have concluded that the annual cycle of this species "is governed by the periodicity of internal reproductive rhythms in combination with multiple annual cyclic environmental factors, including photoperiod, ambient temperature, rainfall and social influences." In captives kept indoors under conditions of constant artificial day length and temperature, normal ovulatory cyclicity and normal birth cyclicity persisted for at least 12 years. Further studies revealed that experimental manipulation of the photoperiod experienced by captive females had little or no effect on the females' natural ovulatory cycles (Nozaki et al. 1992, p. 309). Simultaneous manipulation of photoperiod and temperature yielded equivocal results; these simultaneous manipulations succeeded in reversing the natural ovulatory cycles in two of four experimental monkeys (Nozaki et al. 1992, p. 310).

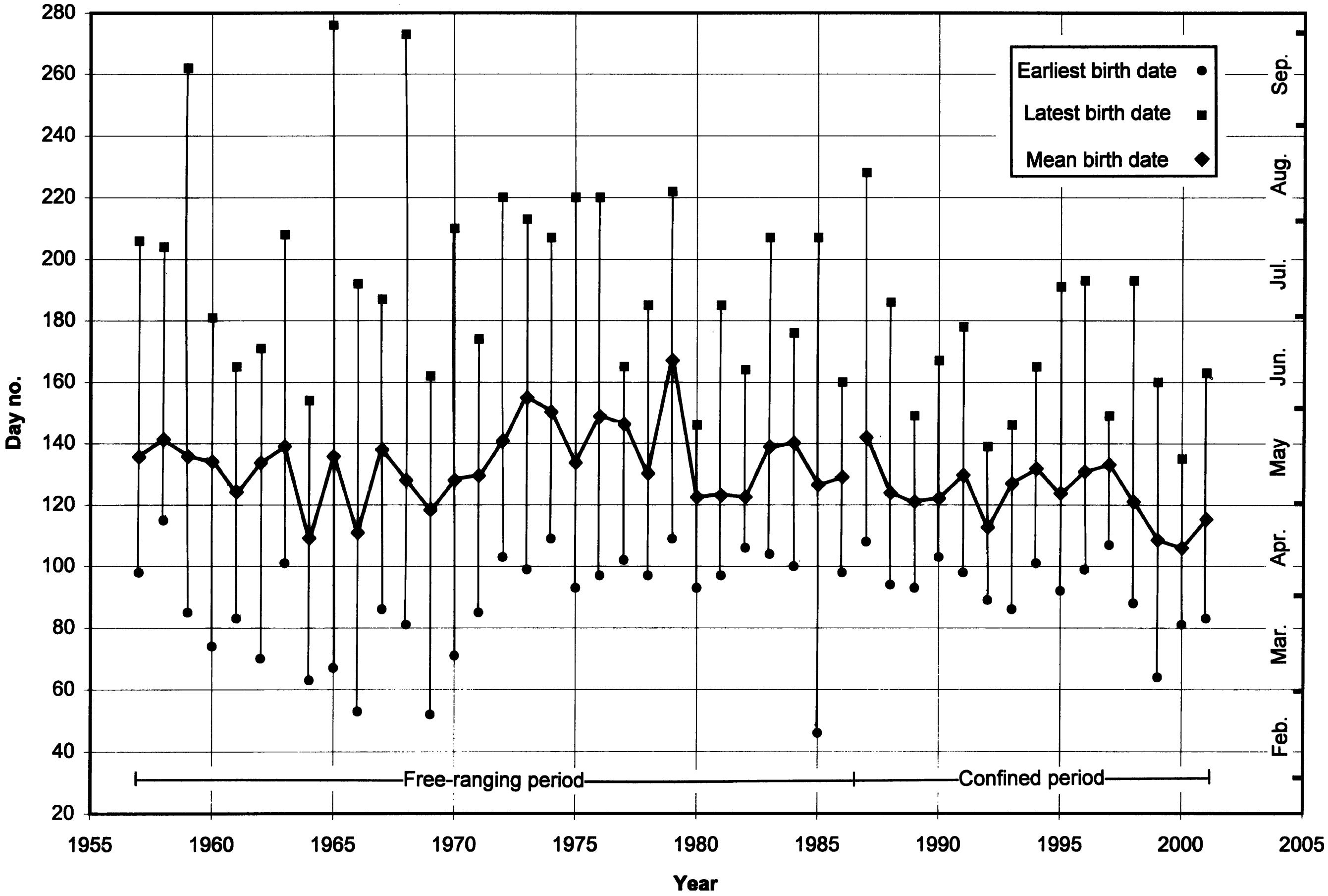

Fig. 3 Interannual variation in mean birth date in an *M. fuscata* population translocated from Yakushima to Ohirayama, Honshu, in 1957 and to nearby Japan Monkey Centre in 1997; this population was free ranging until August 1986 and subsequently has been confined to enclosures. For documentation, see Appendix 2

Discussion

Laboratory studies indicate that *M. fuscata* females manifest an intrinsic reproductive rhythm that can persist independently of external photoperiod or temperature cues. This intrinsic rhythm also is evident in free-ranging troops that have been translocated across up to 11° of latitude and nonetheless have maintained their original reproductive cycles virtually unchanged (Table 1); translocation of a troop from Japan to the southern hemisphere, however, has resulted in reversal of the original northern hemisphere cycle – presumably in response to the reversed seasons.

Available information concerning in-situ *M. fuscata* troops that inhabit the latitudinal zone between Toimisaki (31°22′N) and Kinkazan (38°17′N) suggests that the intrinsic reproductive rhythm of these troops has become locally coordinated with some aspect of latitudinal variation and that the mean birth date in these troops tends to become earlier as the latitude of troop localities increases (Fig. 2). However, in troops that have been sampled south of Toimisaki (i.e., Nina-A, Yakushima) and north of Kinkazan (i.e., Wakinosawa, Shimokita Hanto), the mean birth date apparently does not have the same relationship to latitude as in troops within the Toimisaki–Kinkazan latitudinal zone. Following are speculative answers to two major questions that arise concerning latitudinal variation in mean birth date in *M. fuscata*.

(1) In *M. fuscata* troops that inhabit the Toimisaki–Kinkazan latitudinal zone, why is it apparently adaptive for the mean birth date to become earlier as the latitude of troop localities increases?

Winter, which generally arrives earlier at higher latitudes than at lower latitudes, is the poorest food season for Japanese macaques (Suzuki 1965, p. 42; Iwamoto 1982, p. 168; Nakagawa 1997, p. 275; Agetsuma and Nakagawa 1998, p. 285). If infants have not reached a minimum level of development before the onset of winter, they presumably will be unlikely to survive the poor food conditions of that season (cf. Eaton 1978, p. 37); poor food conditions affect the survival of infants directly and indirectly, via their lactating mothers. Therefore, it is adaptive for Japanese macaques living at higher latitudes – with earlier winters – to give birth earlier than those living at lower latitudes; as a result of this adaptation, when winter begins, infants born at higher latitudes will be at the same level of development as those born at lower latitudes.

(2) Why does the above relationship between mean birth date and latitude not apply to *M. fuscata* troops on Yakushima (south of Toimisaki) and on Shimokita Hanto (north of Kinkazan)?

Yakushima and Shimokita Hanto are geographically marginal to the main distribution of *M. fuscata* (Fig. 1), and, as a result, monkey troops living in these two areas are affected by special ecological conditions; significantly, during the last glacial maximum, Shimokita Hanto apparently was completely uninhabitable by *M. fuscata* (Tsukada 1982, p. 1092; Kawamoto 1997, p. 37, 1998, p. 54, 1999, p. 303; Takahara et al. 2000, p. 673). Winters on Yakushima are relatively mild (Agetsuma and Nakagawa 1998, p. 276) and therefore are less of a factor in infant survival than elsewhere in the range of *M. fuscata*. Shimokita Hanto, by contrast, is so far north (ca. 41°N) that extrapolation of the Toimisaki–Kinkazan regression to this locality is biologically unfeasible; the mean birth date predicted at this latitude by the Toimisaki–Kinkazan regression is 22 March, which would be well before the end of winter on Shimokita Hanto.

The 2-month difference in mean birth dates between the Nina-A (Yakushima) troop and the Toimisaki and Kojima troops is particularly striking and puzzling, because these localities are in close geographic proximity and therefore are fairly similar in climate (Figs. 1, 2). Additional data collected from in-situ troops at strategically dispersed localities are required to investigate further the patterns and processes of birth-season variation in *M. fuscata*.

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Appendix 1 Birth seasonality in in-situ troops of *M. fuscata*

Locality	Island	Latitude (N)	Longitude (E)	Earliest birth	Latest birth	Mean birth	No. births	Observation years	References[a]
Latitude 31–37°N (localities studied by Kawai et al. 1967, pp. 38–39)									
Toimisaki	Kyushu	31°22′	131°20′	May	August	30 June	105	1958–1961, 1966	1
	Kojima[b]	31°27′	131°23′	20 April	19 September	2 July[c]	262	1952, 1954, 1957–1986	2
Nametoko	Shikoku	33°12′	132°38′	April	July	28 May	466	1963–1966	1
Takasakiyama	Kyushu	33°15′	131°31′	April	October	3 July	1067	1958–1966	1
Kochi	Honshu	34°28′	132°53′	April	July	7 June	24	1958–1959	1
Choshikei	Shodoshima	34°29′	134°11′	March	June	24 April	149	1958, 1960–1962, 1966	1
Rosando	Shodoshima	34°31′	134°19′	March	June	10 May	80	1958–1960, 1962	1
Hagachi	Honshu	34°41′	138°45′	May	July	1 June	9	1966	1
Gagyusan	Honshu	34°48′	133°37′	April	August	27 May	243	1956–1966	1
Funakoshiyama	Honshu	34°51′	134°19′	March	June	28 April	72	1965–1966	1
Minoo-A	Honshu	34°51′	135°29′	April	July	24 May	265	1957, 1958–1966	1
Taishakukyo	Honshu	34°52′	133°14′	April	July	23 May	39	1958–1962	1
Kanbanotaki	Honshu	34°54′	133°37′	April	July	16 May	27	1962	1
Arashiyama	Honshu	35°00′	135°41′	April	August	26 May	220	1957–1966	1
Takagoyama-S	Honshu	35°12′	139°59′	March	July	22 May	69	1959–1963, 1965–1966	1
Takagoyama-A	Honshu	35°14′	140°01′	April	June	23 May	16	1966	1
Jigokudani[d]	Honshu	36°44′	138°25′	27 March	12 July	11 May[e]	108	1963–1975	3
Latitude < 31°N or > 37°N									
Nina-A[f]	Yakushima	30°21′	130°23′	14 March	early July	30 April[g]	> 22[h]	1976–1978,1997–1998, 2000–2002	4
KinkazanA	Kinkazan	38°17′	141°34′	6 April	27 June	26 April[i]	> 12	1966, 1998, 2000	5
Wakinosawa[j]	Honshu	41°08′	140°49′	mid February[k]	early August	13 May[l]	109[m]	1965–1966, 1987–2001	6
Supplementary localities									
Kaminada	Awajishima	34°15′	134°54′	mid May	late August		606	1978–1995	7
Katsuyama	Honshu	35°05′	133°38′	March	August		914	1958–1986	8

Appendix 1 (Continued)

Locality	Island	Latitude (N)	Longitude (E)	Earliest birth	Latest birth	Mean birth	No. births	Observation years	References[a]
Hakone	Honshu	35°11′	139°02′	April	October		149	1971–1977	9
Ryozen-A	Honshu	35°17′	136°23′	April	July		54	1971–1975	10
Otoumi	Honshu	35°32′	135°29′	10 May	1 August			1972–1973	11

[a] Key to references: 1 Kawai et al. 1967, pp. 38–39. 2 Field Research Center archives, Primate Research Institute, Kyoto University (PRIKU); cf. Kawai et al. 1967, p. 39; Mori et al. 1997, p. 570. 3 Tokita and Hara 1975, pp. 32–33; cf. Kawai et al. 1967, p. 38. 4 S. Hayaishi, PRIKU, 2 unpublished records; S. Hayakawa, PRIKU, 10 unpublished records; J. Soltis, National Institutes of Health, U.S.A., 10 unpublished records; cf. Maruhashi 1982, p. 323; Soltis et al. 2000, p. 196. 5 S. Fujita and H. Sugiura, PRIKU, 12 unpublished records; cf. Kawai et al. 1967, p. 39. 6 Koford 1969, p. 12; Azuma 1985 p. 3; Dr. Shirou Matsuoka, Working Group for Monkeys in the Shimokita Peninsula, 101 unpublished records; cf. Kawai et al. 1967, p. 39. 7 Nakamichi 1989, p. 738; Nakamichi et al. 1997, p. 227. 8 Itoigawa et al. 1992, p. 58. 9 Fukuda 1988, p. 480. 10 Sugiyama and Ohsawa 1982, p. 242. 11 Watanabe 1978, p. 37

[b] Kojima = Koshima

[c] SD = 27.0 days

[d] Jigokudani = Shiga A

[e] SD = 18.4 days

[f] Data for this locality include records of two births in nearby B troop

[g] SD = 25.8 days

[h] Includes four estimates: 6 May–10 June (i.e. ca. 24 May, two births); "middle of June" (i.e. ca. 15 June); and "end of June" (i.e. ca. 26 June)

[i] SD = 22.7 days

[j] Include stroops A2-85 and A87, observed at Wakinosawa, Shimokita Hanto [Peninsula]

[k] Includesone unusually early birth date (mid February 1988); the next earliest birth date recorded at this locality is 30 March (1998)

[l] SD = 22.0 days

[m] Includes 68 estimates; birth dates reported as "early," "middle," and "late" in months are estimated to have occurred on the 6th, 15th, and 26th days, respectively, of those months (e.g. "early May" is estimated as 6 May)

Appendix 2 Birth-season statistics for a *M. fuscata* population translocated in 1957 from Yakushima to Ohirayama, Honshu, and translocated in 1997 to nearby Japan Monkey Centre (cf. Fig. 3); source: Japan Monkey Centre archives, courtesy of A. Katoh

Year	Mean birth date	SD (days)	*n*	Extreme birth dates	Year	Mean birth date	SD (days)	*n*	Extreme birth dates
Free-ranging period (1957–1986)									
1957	15 May	37.1	9	8 April–25 July	1972	19 May	27.4	27	12 April–7 August
1958	21 May	35.8	5	25 April–23 July	1973	3 June	38.7	16	9 April–1 August
1959	15 May	63.6	6	26 March–19 September	1974	30 May	34.9	10	19 April–26 July
1960	13 May	25.6	19	14 March–29 June	1975	13 May	36.2	10	3 April–8 August
1961	4 May	21.4	13	24 March–14 June	1976	27 May	32.9	10	6 April–7 August
1962	13 May	23.0	25	11 March–20 June	1977	26 May	20.5	9	12 April–14 June
1963	19 May	26.3	14	11 April–27 July	1978	10 May	29.9	11	7 April–4 July
1964	18 April	22.3	26	3 March–2 June	1979	16 June	38.6	8	19 April–10 August
1965	15 May	43.4	20	8 March–3 October	1980	1 May	18.2	10	2 April–25 May
1966	20 April	29.2	24	22 February–11 July	1981	3 May	26.8	11	7 April–4 July
1967	17 May	26.5	25	27 March–6 July	1982	2 May	22.2	7	16 April–13 June
1968	7 May	38.8	25	21 March–29 September	1983	18 May	24.6	14	14 April–26 July
1969	28 April	27.4	23	21 February–11 June	1984	19 May	23.7	8	9 April–24 June
1970	8 May	31.1	29	12 March–29 July	1985	6 May	37.1	14	15 February–26 July
1971	9 May	24.9	16	26 March–23 June	1986	9 May	20.2	14	8 April–9 June
					Totals	12 May	31.7	458	15 February–3 October
Confined period (1987–2001)									
1987	22 May	31.1	13	18 April–16 August	1995	3 May	27.7	15	2 April–10 July
1988	2 May	24.6	13	3 April–4 July	1996	9 May	24.5	15	8 April–11 July
1989	1 May	17.7	15	3 April–29 May	1997	13 May	16.1	8	17 April–29 May
1990	2 May	21.4	8	13 April–16 June	1998	1 May	30.2	12	29 March–12 July
1991	9 May	21.4	14	8 April–27 June	1999	18 April	27.8	13	5 March–9 June
1992	21 April	18.9	9	29 March–18 May	2000	15 April	17.8	14	21 March–14 May
1993	7 May	20.3	13	27 March–26 May	2001	25 April	24.1	21	24 March–12 June
1994	11 May	23.2	9	11 April–14 June	Totals	3 May	24.8	192	5 March–16 August

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