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Troop Composition Data of Wild Japanese Macaques Reviewed by Multivariate Methods

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ABSTRACT. The troop composition (numbers of adult males, X_1, adult females, X_2, juveniles, X_3, and infants, X_4) of the Japanese macaque, *Macaca fuscata,* was examined using principal component analysis and discriminant analysis with 35 data sets from its entire distribution range. X_2, X_3 and X_4 showed an equally high, positive correlation with one another. The variations of the troop composition variables were reinterpreted by a component representing the troop "size" and those representing "shape." The data sets were sorted into three habitat zone groups from north to south. The functions discriminating between the habitat zone groups indicated that X_2 and X_4 largely suffice for the discrimination. Examination of X_2 and X_4 revealed that the troops in the south have a greater X_4/X_2 ratio; however, further examination of this result indicated a relatively high offspring/female ratio only in the disturbed middle habitat zone but no conclusive latitudinal difference of birth rate. The results were discussed in relation to socioecology of the species.

INTRODUCTION

Population dynamics of Japanese macaques (*Macaca fuscata*) has been studied mostly on a single or a few fissioned troops. There have been several intensive studies on provisioned troops (e.g., MASUI et al., 1973, 1975; SUGIYAMA & OHSAWA, 1974, 1982; KOYAMA, NORIKOSHI & MANO, 1975; OHSAWA & SUGIYAMA, 1980) and a few successful studies on wild troops (MARUHASHI, 1982; IKEDA, 1982). The situation is similar in other well-studied macaque species (e.g., *M. mulatta*: DRICKAMER, 1974; SOUTHWICK & SIDDIQI, 1976; SADE et al., 1976; TEAS et al., 1981; SMITH, 1982; *M. sinica*: DITTUS, 1975).

The long research history of the Japanese macaque, as reviewed by BALDWIN, KOYAMA and TELEKI (1980) and KAWAI and OHSAWA (1983), provides a rare opportunity for intertroop comparison. However, most demographic data obtained from wild troops are rough and unsuitable for analyses based on ordinary population models. For such data, largely inductive multivariate statistical methods (e.g., MORRISON, 1976; KENDALL, 1980) may be useful as JORDE and SPUHLER (1974) showed in an interspecific quantitative analysis of primate socioecology. This paper applies principal component analysis and discriminant analysis to the troop composition data of wild Japanese macaques and attempts to overview the variation of troop composition in this species.

MATERIALS AND METHODS

MASUI (1976, 1979) extensively reviewed troop composition data obtained from the entire

1) Order of authorship determined by a flip of a coin.

distribution range of the Japanese macaque. In Table 1, modified and expanded from MASUI's reviews, 35 sets of composition data from wild (non-provisioned) troops are arranged and numbered from north to south according to the locations of the troops (mapped in BALDWIN, KOYAMA & TELEKI, 1980). The study period and reliability of the data vary from study to study; nevertheless the general trends are expected to be retained. Note that the data are mostly of winter for the northern troops and of late spring or summer for the southern troops.

As to age-sex classes for describing the troop composition, four classes are used here: adult male, adult female, juvenile and infant. If the original source uses more divisions, the following grouping is employed: adult males include adolescent or subadult males (roughly >5 years); adult females include adolescent or subadult females (roughly >5 years); juveniles are >1 year; and infants are <1 year. Thus the composition of a troop is represented by the four-dimensional vector $\boldsymbol{X} = (X_1, X_2, X_3, X_4)$, where X_1 denotes the number of adult males of the troop, X_2 that of adult females, X_3 that of juveniles and X_4 that of infants. Also the vector $\boldsymbol{x} = (x_1, x_2, x_3, x_4)$, where $x_i = (X_i - \hat{X}_i)/\hat{s}_i$, $\hat{X}_i$ and $\hat{s}_i$ being the mean and standard deviation estimates, is sometimes used instead of $\boldsymbol{X}$.

The vegetation within the Japanese macaque's distribution range can be roughly divided into two major zones: the deciduous broadleaf forest (cool temperate) zone in the north, which mostly overlaps with the snowy zone, and the evergreen broadleaf forest (warm temperate or partly subtropical) zone in the south (SUZUKI, 1965; UEHARA, 1975; TAKASAKI, 1981a, b). Data Nos. 1–10 are in the deciduous zone and the rest are in the evergreen zone. However, most habitats in southern Honshu are covered with secondary deciduous or deciduous/evergreen intermediate vegetation due to human activities or poor soil (TAKASAKI, 1981a, b). Here the troops in the evergreen zone are subdivided into those in the middle zone (11–21) and those in the further south (22–35). Thus from north to south, there are three zones: North zone (snowy and deciduous; 1–10), Middle zone (secondary deciduous or deciduous/evergreen; 11–21), and South zone (evergreen; 22–35). In particular, the studies from Yakushima Island (25–35) constitute most of the data from the South zone.

The multivariate statistical methods used were principal component analysis and discriminant analysis. As the discriminant function, the Wald-Anderson classification statistic (see MORRISON, 1976) was used. The respective Fortran programs given in BOLCH and HUANG (1974) were used with modifications. The calculations were processed by FACOM M-382 system of the Data Processing Center, Kyoto University.

RESULTS

The correlation matrix of the troop composition variables, X_1, X_2, X_3 and X_4, is shown in Table 2. The variables are highly correlated with one another except for X_1. The coefficients and variances of the four components extracted from this matrix are summarized in Table 3. The first principal component, $z_1 = 0.34x_1 + 0.56x_2 + 0.55x_3 + 0.53x_4$, accounts for 75% of the variance in the four dimensions. The "size" of troops could be characterized by this variable. The other three components could be interpreted as measures of troop "shape"; e.g., the second component characterizes the number of adult males in particular. However, the fact that the high, positive correlations between X_2, X_3 and X_4 are nearly equal indicates little interpretive value of the third and fourth components; i.e., they are probably isotropic. The component correlation coefficients are given in Table 4. The results obtained from the

Table 1. Troop composition* of wild Japanese macaque from north to south, modified and expanded from MASUI (1976, 1979).

Data No.	Locality (latitude N)	Troop name (date)	X_1	X_2	X_3	X_4	$\sum_i X_i$	X_1/X_2	X_4/X_2	Source
1	Shimokita NW (41°30′)	M (Dec. 1970)	5	13	13	5	36	0.38	0.38	IZAWA (1971)
2		Z (Mar.–Apr. 1972)	7	18	10	7	42	0.39	0.39	IZAWA (1972)
3	Shimokita SW (41°10′)	O (Mar. 1963)	4	4	3	2	13	1.00	0.50	IZAWA & NISHIDA (1963)[1)]
4		A_2 (Mar. 1979)	6	16	21	3	46	0.38	0.19	ASHIZAWA (1979)
5	Shiga Heights (35°35′)	B_2 (Apr.–May 1975)	8	6	4	1	19	1.33	0.17	SUZUKI et al. (1975)
6		YB_1 (Oct. 1969)	6	19	15	5	45	0.32	0.26	YOSHIHIRO et al. (1979)
7	Hakusan Mts. (36°15′)	KA (Nov. 1970)	9	16	14	6	45	0.56	0.38	KAWAI et al. (1970)[1)]
8		TA (Jan.–Feb. 1975)	20	22	14	8	64	0.91	0.36	IZAWA (1978)
9		TB (Jan.–Feb. 1975)	10	20	12	4	46	0.50	0.20	IZAWA (1978)
10		O (Jan.–Feb. 1975)	12	18	16	7	53	0.67	0.39	IZAWA (1978)
11	Otoumi (35°30′)	A (Aug. 1972)	6	23	35	11	75	0.26	0.48	WATANABE (1978)
12	Takagoyama (35°10′)	T-Ib (1970)	6	15	28	7	56	0.40	0.47	YOTSUMOTO (1976)
13	Yugawara (35°10′)	T (1964)	13	19	12	2	46	0.68	0.11	MURAMATSU & FUKUDA[1)]
14		P (1963)	3	10	3	2	18	0.30	0.20	NODA[1)]
15	Minoo (34°50′)	A (1955)	6	22	41	17	86	0.27	0.77	KAWAMURA (1956)[1)]
16		B (1955)	1	5	8	3	17	0.20	0.60	KAWAMURA & KAWAI (1956)[1)]
17	Gagyusan[2)] (34°50′)	(1956)	10	35	50	25	120	0.29	0.71	FURUYA (1956)[1)]
18	Shodoshima (34°30′)	I (May 1962)	48	37	35	9	129	1.30	0.24	YAMADA (1966)[1)]
19		K (May 1957)	17	41	72	31	161	0.41	0.76	YAMADA (1966)[1)]
20		O (May 1957)	13	17	13	9	52	0.76	0.53	YAMADA (1966)[1)]
21		T (1957)	11	15	17	9	52	0.73	0.60	YAMADA (1966)[1)]
22	Gokashowan-Tsubonegacho (34°20′)	(Aug. 1979)	4	13	16	9	42	0.31	0.69	MASUI (1980)
23	Kawaradake (33°40′)	(Jan. 1973)	7	33	41	21	102	0.21	0.64	IKEDA et al. (1973)
24	Koshima[2)] (31°30′)	(Aug. 1952)	4	6	9	3	22	0.67	0.50	ITANI & TOKUDA (1958)[1)]

(continued)

Table 1. (continued)

Data No.	Locality (latitude N)	Troop name (date)	X_1	X_2	X_3	X_4	$\sum_i X_i$	X_1/X_2	X_4/X_2	Source
25	Yakushima (30°20′)	Ko (Aug. 1976)	12	18	11	6	47	0.67	0.33	Maruhashi (1980)
26		Todai (Aug. 1978)	7	7	9	4	27	1.00	0.57	Maruhashi (1982)
27		Kannon (Oct. 1977)	4	4	3	2	13	1.00	0.50	Maruhashi (1982)
28		Hanyama (June 1976)	12	12	15	6	45	1.00	0.50	Maruhashi (1982)
29		Nina (Aug. 1978)	7	10	5	3	25	0.70	0.30	Maruhashi (1982)
30		Kawara (July 1975)	4	6	5	2	17	0.67	0.33	Maruhashi (1982)
31		Shikamizawa (Aug. 1978)	8	8	9	3	28	1.00	0.38	Maruhashi (1982)
32		M (May 1979)	5	7	6	4	22	0.71	0.57	Maruhashi (1982)
33		A (May 1979)	7	8	11	5	31	0.88	0.63	Maruhashi (1982)
34		H (May 1979)	3	3	3	2	11	1.00	0.67	Maruhashi (1982)
35		M (May 1981)	7	8	8	4	27	0.88	0.50	Furuichi (1983)
Total			312	534	587	247	1680			

*Numbers of adult males (X_1), adult females (X_2), juveniles (X_3) and infants (X_4); troop size ($\sum_i X_i$), socionomic sex ratio (X_1/X_2), and infant/female ratio (X_4/X_2). 1) Cited in Masui (1976, 1979); bibliographical data are not included in the list of references of this paper; 2) isolated troop.

Table 2. Correlation matrix of troop composition variables.

	X_1	X_2	X_3	X_4
X_1 (No. of adult males)	1.00	0.61	0.37	0.25
X_2 (No. of adult females)		1.00	0.88	0.83
X_3 (No. of juveniles)			1.00	0.94
X_4 (No. of infants)				1.00

Table 3. Troop composition component coefficients.

	Component			
Variable	1	2	3	4
X_1 (No. of adult males)	0.34	0.88	0.33	0.08
X_2 (No. of adult females)	0.56	0.10	−0.82	0.04
X_3 (No. of juveniles)	0.55	−0.26	0.31	−0.73
X_4 (No. of infants)	0.52	−0.39	0.34	0.67
Variance	3.01	0.85	0.08	0.06

Table 4. Correlation of troop composition variables and components.

	Component			
Variable	1	2	3	4
X_1 (No. of adult males)	0.58	0.81	0.10	0.02
X_2 (No. of adult females)	0.97	0.09	−0.24	0.01
X_3 (No. of juveniles)	0.95	−0.24	0.09	−0.17
X_4 (No. of infants)	0.91	−0.36	0.10	0.16

components extracted from the covariance matrix are similar, and they are not presented here.

When the three habitat zone groups—North zone, Middle zone and South zone groups—are distinguished, two linearly independent discriminant functions are determined as:

$$W_{NM} = -0.03X_1+0.17X_2-0.13X_3-0.34X_4+2.45$$

and

$$W_{NS} = 0.01X_1+0.07X_2-0.03X_3-0.12X_4-0.06\ ,$$

where W_{NM} denotes the Wald-Anderson classification statistic for the *N*orth zone and *M*iddle zone groups, etc. These functions lead to the classification summarized in Table 5, where ten data points (29%) are misclassified. None of the pairs of groups is shown to have significantly different mean vectors (Hotelling's T^2 between the *N*orth zone and *M*iddle zone groups, $T^2_{NM} = 17.3$, $F_{4,16} = 2.2$; $T^2_{NS} = 2.4$, $F_{4,19} = 0.4$; $T^2_{MS} = 13.2$, $F_{4,20} = 2.1$); the discriminant efficiency is nonsignificant.

When the North zone and Middle zone groups are combined into one group, the function discriminating between the combined North-Middle zone group and the South zone group is determined as:

$$W = -0.11X_1+0.30X_2+0.08X_3-0.41X_4-1.94\ .$$

This function leads to the classification summarized in Table 6, where seven data points (20%) are misclassified. The negative and greater value of the coefficient of the variable X_1 in comparison with the previous functions is probably due to the consistently high socionomic

Table 5. Summary of classification by the functions discriminating between the three habitat zone groups.

Classification by discriminant functions	Classification by habitat zone[1)]			
	North	Middle	South	Total
North zone	8	2 (13, 14)	3 (25, 29, 30)	13
Middle zone	0	7	1 (23)	8
South zone	2 (1, 3)	2 (16, 20)	10	14
Total	10	11	14	35

1) Figures in parentheses indicate the misclassified data Nos. (see Table 1).

Table 6. Summary of classification by the function discriminating between two groups (North zone and Middle zone grouped together).

Classification by discriminant function	Classification by habitat zone[1)]		
	North-Middle	South	Total
North-Middle zone	16	2 (23, 25)	18
South zone	5 (3, 5, 16, 20, 21)	12	17
Total	21	14	35

1) Figures in parentheses indicate the misclassified data Nos. (see Table 1).

sex ratio (X_1/X_2) in the South zone group (see Table 1). The two groups have significantly different mean vectors ($T^2 = 14.3$, $F_{4,30} = 3.2$, $p<0.05$). When the Middle zone and South zone groups are combined in comparison with the North zone group, the discrimination is less successful; eight data points (23%) are misclassified. The mean vector does not differ significantly between the two groups ($T^2 = 10.9$, $F_{4,30} = 2.5$).

With a positive weighting coefficient of X_2 (number of adult females) and negative coefficient of X_4 (number of infants), all W's above incorporate some function of difference between the two variables, i.e., some measure of natality. Examination of the infant/female ratios (X_4/X_2) of the misclassified data points supports this interpretation. As expected, the two-dimensional vector (X_2, X_4) has a significant mean difference between the North-Middle zone group and the South zone group ($T^2 = 10.8$, $F_{2,32} = 5.3$, $p<0.01$), and the decrease in the discriminant efficiency due to the reduction of variables is nonsignificant ($F_{2,30} = 1.2$). The discriminant function is:

$$W = 0.21X_2 - 0.17X_4 - 1.92\,,$$

which misclassifies nine data points (26%). Similarly, the two-dimensional vector composed of the numbers of adult females (X_2) and juveniles (X_3) also gives a significant mean vector difference ($T^2 = 8.1$, $F_{2,32} = 3.9$, $p<0.05$) with a nonsignificant decrease in the discriminant efficiency ($F_{2,30} = 2.3$). The discriminant function is:

$$W = 0.16X_2 - 0.04X_3 - 1.70\,,$$

which misclassifies eight data points (23%).

From these results, North-Middle zone group and the South zone group are expected to be better discriminated from each other with the three variables X_2, X_3 and X_4. These variables have a nearly equal positive correlation with one another as already shown in Table 2. Then we can practically reduce the discriminator of the three-dimensional data to two dimensions by taking an ad hoc pair of uncorrelated "size" and "shape" components (see KENDALL, 1980). By setting $u = x_2+x_3+x_4$ as the size component and $v = 0.329x_2-0.001x_3-0.328x_4$ as the shape component, the discriminant function is determined as:

$$w = 0.18u+2.36v+0.37.$$

This function misclassifies six data points (17%), fewer than any other discriminant function above. Note that the shape component v is virtually a difference between x_2 and x_4 since the weighting coefficient of x_3 is negligible in comparison with those of the others, and that v has a much greater weighting coefficient than u in the discriminant function w. Therefore, the discrimination largely depends on x_2 and x_4.

Thus, of the troop composition data, the numbers of adult females (X_2) and infants (X_4) practically suffice for the discrimination between the North-Middle zone group and the South zone group. Figure 1 plots the points (X_2, X_4) on a log scale and shows the regression lines through the origin ($X_4 = bX_2$, where b is a constant) fitted to the three groups of points sorted by the habitat zone. The regression equations for the North zone group, Middle zone group, and South zone group are respectively $X_4 = 0.315X_2$, $X_4 = 0.548X_2$ and $X_4 = 0.549X_2$. The slope difference is significant between the North zone and the Middle zone groups (Newman-Keuls test, $q_{32,2} = 3.2$, $p<0.05$) and between the North zone and the South zone groups ($q_{32,3} = 4.1$, $p<0.05$), but nonsignificant between the Middle zone and the South zone groups ($q_{32,2} = 0.02$). This result, which suggests that the Middle zone group be lumped together with the South zone group rather than with the North zone group, disagrees with the results of the discriminant analysis above. A closer look at Figure 1 reveals that the number of adult females (X_2) alone largely suffices for the discrimination of the North and Middle zone groups from the South zone group, because the troops in the North and Middle

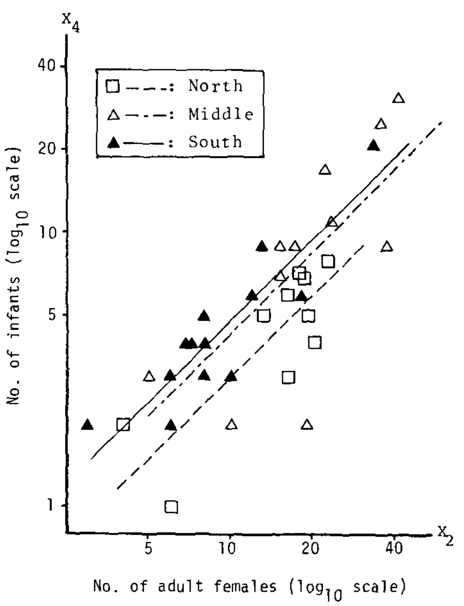

Fig. 1. Three groups of data points for numbers of adult females (X_2) and infants (X_4) within the troop, and their $X_4 = bX_2$ type regression lines.

zone groups, especially those in the Middle zone group, are large-sized and accordingly have large X_2's. The slope (b) of the X_4-on-X_2 regression line represents the troop "shape" but not the troop "size." Therefore, the grouping based on the slope b alone differs from that based on the discriminant analysis.

The difference in the slope b suggests some latitudinal cline of birth rate (higher in the south), if seasonal difference due to the census date is negligible. Further to examine the probability of a cline, regression lines through the origin are determined for the pairs (X_4, X_3) and (X_2, X_3), since the seasonal differences of X_2 and X_3 due to the census date are expected to be less than that of X_4. The X_3-on-X_4 regression equations for the North zone group, Middle zone group, and the South zone group are respectively $X_3 = 2.29X_4$, $X_3 = 2.34X_4$ and $X_3 = 1.98X_4$; but the slopes do not differ significantly ($F_{2,32} = 1.2$). The X_3-on-X_2 regression equations are respectively $X_3 = 0.787X_2$, $X_3 = 1.37X_2$ and $X_3 = 1.09X_2$. The slope difference is significant between the North zone and the Middle zone groups ($q_{32,3} = 5.4$, $p<0.005$), but nonsignificant between the North zone and the South zone groups ($q_{32,2} = 2.3$) and between the Middle zone and the South zone groups ($q_{32,2} = 2.4$). In the X_3-on-X_2 regressions, note that the Middle zone group has the steepest slope, which may indicate a relatively fast population growth. This is probably related to the fact that this group of troops mostly live in disturbed habitats and are large-sized. From these results, a relatively high offspring/female ratio is inferred in the Middle zone group. However, without further reliable data on the death (or survival) rates of adult females, juveniles and infants, there can be concluded neither definite difference between the North zone and South zone groups nor latitudinal cline in the birth rate.

CONCLUSIONS AND DISCUSSION

The results of this study have mostly confirmed the inferences made in previous studies (Masui, 1976, 1979). This study dealt with only 35 data sets; the sample size is not convincingly large. Although additional data may reveal further significant results, the general trends shown here are probably unchanging.

The absence of clear tendency at first sight in the number of adult males (X_1) in comparison with the other troop composition variables is understandable if we see the fact that the socionomic sex ratio (X_1/X_2) is consistently high among the non-isolated troops in relatively undisturbed habitats (e.g., Yakushima Island). Japanese macaque males generally leave their natal troops and join other troops or become solitaries (Nishida, 1966; Norikoshi & Koyama, 1975). Since efficiency of intertroop male transfer probably decreases as the distance and difficulty in travel between troops increase, imbalance of emigrant and immigrant males could occur in isolated troops and those living in disturbed habitats.

Since the numbers of adult females (X_2), juveniles (X_3) and infants (X_4) equally well correlate with one another, only one of them (especially X_2) virtually suffices to represent the troop "size." The ratios of the remaining two variables to the former could be taken as measures of the troop "shape."

There is no prominent troop size difference between the North zone and the South zone, though the Middle zone troops are relatively large-sized. The troop composition variables show no such drastic variation as the per capita home range area (Takasaki, 1981a, b). The variation of troop composition forms a continuum (see Fig. 1).

In an analysis of data from Yakushima Island, Iwano (1983) attempted to explain the relatively small troop size in Yakushima and the cool temperate zone in comparison with the relatively large troop size in the middle warm temperate zone by referring to CROOK's tentative model which relates social systems and environmental variables in cercopithecoids: Medium numerical density and large multimale bisexual reproductive social units are likely to occur in habitats of medium environmental stability (CROOK, 1970). However, habitats in the middle warm temperate zone, if disturbed by human activities, do not necessarily have medium environmental stability. Therefore, CROOK's model is not applicable to the present case without reliable measurement of environmental stability. The observed variation of the Japanese macaque's troop size seems rather correlated with the degree of habitat disturbance; i.e., there is a trend to larger troops in disturbed habitats, although the causality of this trend is unknown.

A latitudinal cline in the infant/female ratio (X_4/X_2) or natality of Japanese macaques has been repeatedly suggested (e.g., MASUI, 1976, 1979; SUGIYAMA & OHSAWA, 1982). Although the present study supported this idea at first, further examination indicated no conclusive latitudinal birth rate difference. When many sets of data on the seasonal and annual changes of troop composition variables (e.g., MARUHASHI, 1982; IKEDA, 1982) become available, this problem can be reexamined. Rather at present, the tendency to a high offspring/female ratio in the disturbed Middle habitat zone is notable. This can be interpreted in the same context as the increased birth rate at Kawaradake after a mass capture of monkeys (IKEDA, 1982). Habitats disturbed by human activities (secondary vegetation, patchy habitat distribution, etc.) would be less saturated than undisturbed habitats with monkeys to the level set by the carrying capacity; a rapid population growth is expected in such a situation (TAKASAKI, 1984).

Demographic data from different troops of one locality are often pooled together to obtain one general life table (e.g., MASUI et al., 1973, 1975; SADE et al., 1976; SMITH, 1982). Macaques are group-living primates, and their unit of reproduction and social life is the troop (ITANI, 1977). A study dealing with intraspecific variations of troop composition could employ different methods as shown in this paper.

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