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Population Genetics of Japanese Monkeys:
I. Estimation of the Effective Troop Size

KEN NOZAWA
Kyoto University

ABSTRACT. In order to estimate the genetically effective troop size of Japanese monkeys, we have to know the pattern of distribution of the numbers of gametes contributed by the individual members of the parental population to the next generation. The author inspected the observation records of macaque troops made by a number of socio-ecologists and found that the relationship between sexual rank and sexual activity of adult males could be approximately expressed by the law of geometrical series. Assuming that the genetic contribution of male parents to the next generation was proportional to their sexual activity and that the numbers of gametes contributed by the female parents formed the POISSON distribution, the author derived a formula for estimating effective troop size (N), namely,

$$N=\frac{4-2/N_c}{\dfrac{5/N_f}{2-5/N_f}\,\dfrac{1+(1-5/N_f)^{N_m}}{1-(1-5/N_f)^{N_m}}+\dfrac{1}{N_f}-\dfrac{1}{N_c}},$$

where N_c was the census number and N_m and N_f the numbers of male and female parents, respectively, of the troop. Moreover, assuming $N_m=0.2N_c$ and $N_f=0.3\ N_c$ as an average, the effective size could be estimated as 36% or less of the census number.

INTRODUCTION

The effective population size is one of the most important conceptions in population genetics. This is defined as the number of breeding adults in an idealized population in which a random gamete has an equal probability of having come from any parent. In a population of a finite size the gene frequency (q) of a polymorphic loci fluctuates at random, independently of systematic evolutionary pressures, that is, selection, recurrent mutation, and migration. The amount of fluctuation which can be measured by sampling variance of binomial distribution ($\sigma^2_{\delta q}$) is given as

$$\sigma^2_{\delta q}=\frac{q(1-q)}{2N},$$

where N is the effective population size. In that population the heterozygous gene loci come to fixation by chance, generation after generation, and the rate of loss of heterozygosis (K), in other words, the effectiveness of chance fixation of genes, is inversely proportional to the effective size, namely

$$K=\frac{1}{2N}$$

(WRIGHT, 1931).

WRIGHT (1938) derived a formula to estimate the effective size (N) of the population in which N_0 parents contributed a varying number (k) of gametes to the next generation, the mean of k being 2, and δ_k the standard deviation of numbers of gametes contributed by the individual parents, namely

$$N = \frac{4N_0 - 2}{\sigma^2{}_k + 2} \, .$$

In the derivation of this formula, however, the inequality of the numbers of breeding males and females and, therefore, the inequality in the pattern of distribution of numbers of progeny between male and female parental populations, has not been specifically considered. Thus, some inconveniences are experienced in applying this formula in estimating the effective sizes of populations of livestock and other kinds of animals in which the parental sex-ratio ordinarily deviates from one to one. The author (1957) derived a formula, to estimate the effective population size of farm animals in which the number of male parents is usually much less than that of female parents.

Now we are interested in obtaining the effective size of Japanese monkey troops as a genetic parameter indispensable for the understanding of the evolutionary dynamics of this species. In Japanese monkey troops such special circumstances exist that the father of an individual can not be known. These circumstances make it difficult to estimate the effective troop size. But, on the other hand, it is well-known that the troop is integrated socially by the rank system among its individual members. The existence of this social rank system, especially among adult males, should give us a clue for estimating the effective troop size, overcoming at least partially the above stated difficulty. In the present paper the author will bring forward a mathematical formulation for, and the results of, the estimation of the genetically effective size of Japanese monkey troops.

GENERAL FORMULA AND DISTRIBUTION OF THE GAMETE CONTRIBUTION OF THE FEMALE PARENTS

Consider the autosomal genes. Let us start with a parental population of N_m males and N_f females, and consider the distribution of the numbers of gametes contributed by the individual members of the parental population: in the male parents the i-th male contributes k_{mi} gametes, and in the female parents the j-th female contributes k_{fj} gametes to the next generation. If we define one generation as the period of time required for reproduction of the present census number of the population (N_c), then

$$\sum_i k_{mi} = \sum_j k_{fj} = N_c \, . \qquad (1)$$

When we take a random sample of two gametes from the set of gametes coming from the parental population to the progeny population, the probability that these two have been contributed by the same parent is

$$\frac{\sum_i k_{mi}(k_{mi} - 1) + \sum_j k_{fj}(k_{fj} - 1)}{2N_c(2N_c - 1)} \, .$$

If the effective size is N, it is clear from the definition of this measure that the above probability is nearly $1/N$. Thus

$$N=\frac{2N_c(2N_c-1)}{\sum_i k_{mi}(k_{mi}-1)+\sum_j k_{fj}(k_{fj}-1)}$$

$$=\frac{2N_c(2N_c-1)}{\sum_i k^2{}_{mi}-\sum_i k_{mi}+\sum_j k^2{}_{fj}-\sum_j k_{fj}}. \tag{2}$$

We can assume that the distribution of the numbers of gametes contributed by the female parents is of the POISSON type. Therefore, from the well-known property of the POISSON distribution,

$$\sum_j k^2{}_{fj}=N_f\left\{\left(\frac{N_c}{N_f}\right)^2+\frac{N_c}{N_f}\right\}=\frac{N_c{}^2}{N_f}+N_c\,. \tag{3}$$

Here, in order to estimate the effective population size, we have only to calculate $\sum_i k^2{}_{mi}$; this is the problem concerning the type of distribution of the number of gametes contributed by the individual male parents.

DISTRIBUTION OF THE GAMETE CONTRIBUTION OF MALE PARENTS

In order to clarify the distribution of the gametes contributed by male parents, the identification of the male parent of each new-born individual is usually necessary, which is hopelessly difficult to determine in free ranging monkey troops. But, on the other hand, the existence of rank among male adults has some utilitarian value in clarifying this distribution. The author collected quantitative observation records of the sexual activity of adult males in free ranging monkey troops. He wanted to collect only data on Japanese monkeys (*Macaca fuscata*), but such quantitative data were so meagre that he was forced to include several rhesus monkey (*Macaca mulatta*) data in his collection. Table 1 lists the collection.

We can arrange the adult males of a troop in a decreasing order, according to their sexual activity, the measures of which are the number of consort relations, the number of females possessed, the number of copulations, the number of days of copulation, etc., as shown in Table 1. For the methods of enumerating these measures of sexual activity, refer to the respective original papers. The rank observed in this way can be defined as sexual rank. The sexual rank of individual males would not necessarily coincide with their social rank as defined by socio-ecologists. The author tried to evaluate the correlation between these two kinds of rank by calculating SPEARMAN's rank correlation coefficients (cf. KOMATSU, 1949). The results are presented in Table 1. The rank correlation coefficients are always positive and are observed to be very high, especially when the number of adult males is small.

Figure 1 shows graphically the relationship between the sexual rank of adult males, on the abscissa, and the measurement of their sexual activity, on the ordinate, in the 22 sample troops. From these graphs we can see that the difference in sexual activity between two contiguous males is generally larger in higher ranks than in lower ranks; the sequence of points, which decreases monotonously, converges to the abscissa. As a mathematical model of such a pattern we can consider the geometrical sequence: $a_1, a_2, a_3, \ldots\ldots, a_t=a_1, a_1r, a_1r^2, \ldots\ldots, a_1r^{t-1}$. $(0<r<1)$.

The common ratio, r, can be calculated from the observed values as

Table 1. Correlation coefficient between social and sexual ranks of adult males, and the common ratio (r) of the geometric series expressing the relationship between sexual rank and sexual activity of adult males in various Macaca troops.

Species (troop)		Number of adult Males	 Females	Measurement of sexual activity of adult males	Data cited from	Rank correlation coefficient	Common ratio (r)
1	*M. mulatta* (Santiago III)	2	4	No. of consort relationships	Carpenter (1942)	+1.0000	0.0571
2	*M. mulatta* (Santiago III)	2	5	No. of females possessed	Carpenter (1942)	+1.0000	0.1428
3	*M. mulatta* (Santiago IV)	2	6	No. of consort relationships	Carpenter (1942)	+1.0000	0.3437
4	*M. mulatta* (Santiago IV)	2	7	No. of females possessed	Carpenter (1942)	+1.0000	0.5000
5	*M. fuscata* (Koshima)	5	9	No. of copulations	Tokuda (1961–2)	+0.9858	0.5135
6	*M. fuscata* (Koshima)	6	11	No. of sexual relationships	Tokuda (1961–2)	+0.9858	0.5428
7	*M. mulatta* (Santiago I)	8	18	No. of consort relationships	Carpenter (1942)	+0.9762	0.6707
8	*M. mulatta* (Santiago I)	8	17	No. of females possessed	Carpenter (1942)	+0.9762	0.7500
9	*M. fuscata* (Miyajima)	8	16	No. of consort relationships	Hayashi (unpubl.)	+0.6191	0.6272
10	*M. mulatta* (Santiago II)	9	14	No. of consort relationships	Carpenter (1942)	+0.9877	0.6544
11	*M. mulatta* (Santiago II)	9	15	No. of females possessed	Carpenter (1942)	+0.9879	0.7868
12	*M. mulatta* (Santiago)	11	21	No. of matings	Loy (1971)	+0.2605	0.7849
13	*M. mulatta* (Santiago)	12	31	No. of females possessed	Conaway & Koford (1964)	+0.7834	0.8648
14	*M. mulatta* (Santiago)	12	31	No. of days of copulation	Conaway & Koford (1964)	+0.9125	0.8065
15	*M. mulatta* (Santiago)	13	31	No. of days of copulation	Kaufmann (1965)	+0.7363	0.6515
16	*M. mulatta* (Santaigo)	13	31	No. of females, copulated	Kaufmann (1965)	+0.7396	0.7500
17	*M. fuscata* (Miyajima)	13	21	No. of consort relationships	Hayashi (unpubl.)	+0.7425	0.8225
18	*M. mulatta* (Santiago)	14	31	No. of days of mating behavior	Kaufmann (1965)	+0.7869	0.8148
19	*M. mulatta* (Santiago)	14	31	No. of days of mating behavior	Kaufmann (1965)	+0.8121	0.8703
20	*M. f. yakui* (Ohirayama)	22	43	No. of females sexually related	Kawai (unpubl.)	+0.4000	0.9051
21	*M. f. yakui* (Ohirayama)	22	43	No. of copulations	Kawai (unpubl.)	+0.5000	0.8357
22	*M. f. yakui* (Ohirayama)	22	43	No. of mating behavior	Kawai (unpubl.)	+0.9000	0.7818

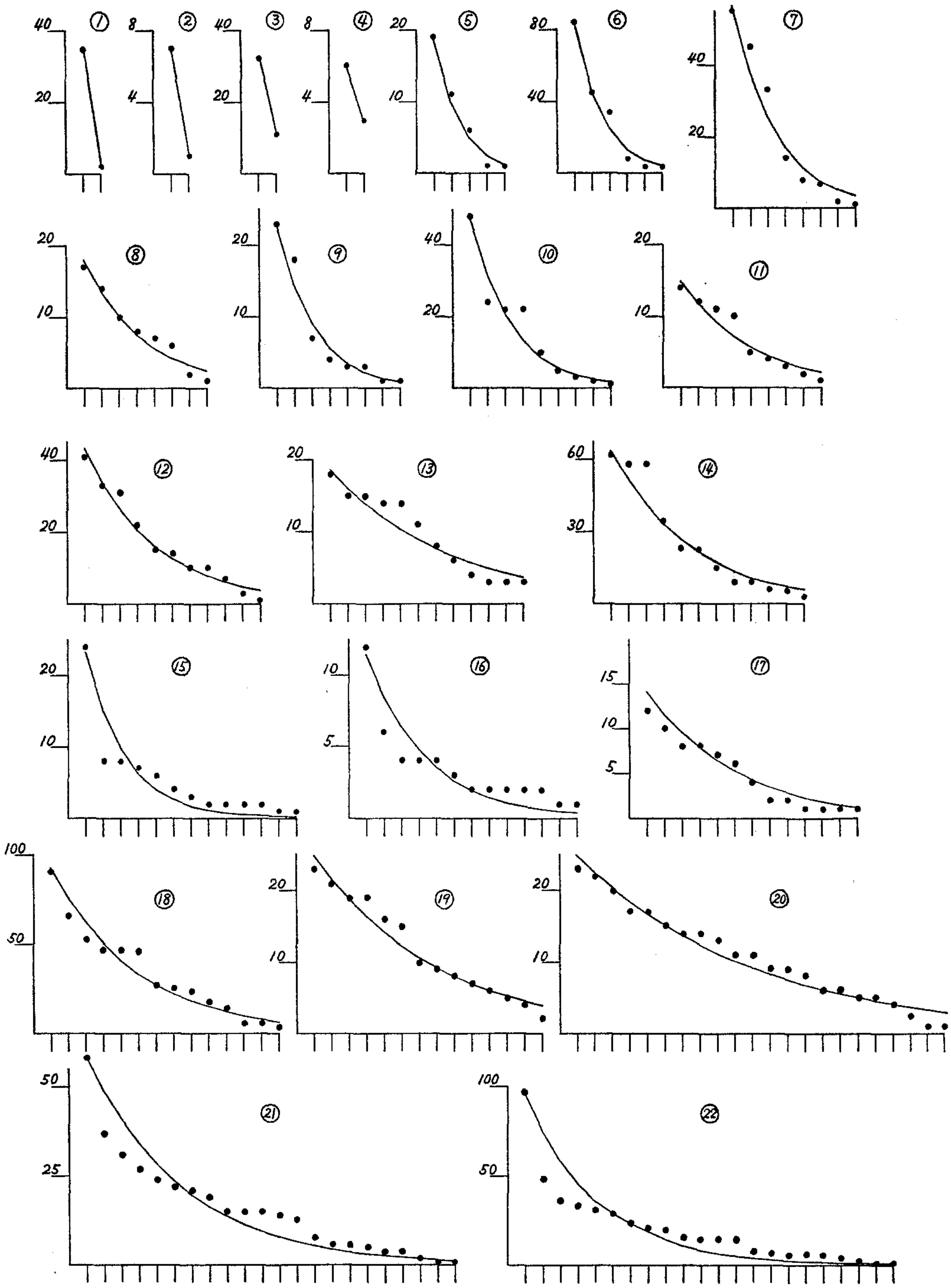

Fig. 1. The relationship between sexual rank of adult males (abscissa) and measurement of their sexual activity (ordinate) in the troop. Encircled numbers in the graph, 1–22, correspond to the troop numbers indicated in Table 1.

$$r = \frac{a_2 + a_3 + \ldots\ldots + a_t}{a_1 + a_2 + \ldots\ldots + a_{t-1}},$$

and the initial term, a_1, as

$$a_1 = \frac{S(1 - r)}{1 - r^t},$$

where $S = a_1 + a_2 + a_3 + \ldots + a_t$. In Figure 1 the expectation curves obtained in this way are also shown. It can be seen that the fitness of the observed sequence of points to the expectation curve are fairly good in each graph.

In the research field of ecology, the so-called "law of geometrical series" has already become known. This law was proposed by MOTOMURA (1932). He showed that in some animal associations the numbers of individuals of species collected in a sample quadrat formed an approximate geometric series when the species were arranged according to the rank of their numbers of individuals. After that several authors (for instance, MOTOMURA, 1935; KATO, 1935; TANAKA, 1948; KATO & HORI, 1952; NOZAWA, 1956) recognized the applicability of this law to the associations of marine animals, rodents, and insects. Moreover, UTIDA (1943) attempted to give a theoretical interpretation to this law. Assuming that (1) each species had an equal initial number (n) of individuals, (2) the habitat was composed of a number (m) of minimum areas where only one individual could exist, (3) the individuals of each species dispersed randomly in the habitat, and (4) only one individual of the strongest species could survive in each minimum area because of the struggle for existence among the species, he showed that the numbers of individuals of the species in the lowering rank came to form a geometric sequence with the initial term n/m and the common ratio $1 - n/m$. To this theory SHINOZAKI & URATA (1953) and SHINOZAKI (1955) presented a criticism, pointing out that the above assumptions (1) and (4) were considered to be biologically unnatural.

Now, let us try to apply UTIDA's theory to the data on the sexual activity of adult males in monkey troops. It would be admitted that the biological unnaturalness criticized by SHINOZAKI & URATA (1953) and SHINOZAKI (1955) is fairly lessened in this case if we consider the troop organization integrated by the rank system among individual members. We consider the 'habitat' in UTIDA's assumption to mean the set of adult females, the number of which is $m = N_f$, and here we can consider that n is a constant relating to the maximum sexual potency of adult males peculiar to the macaque species.

We can test the applicability of UTIDA's theory to the monkey troops as follows. If it is applicable, then

$$r = 1 - \frac{n}{N_f},$$

the larger the number of adult females (N_f), the closer should be the common ratio (r) to unity. This tendency can be clearly observed in Table 1; therefore, we can consider that the applicability of UTIDA's theory has been supported, if not verified, by this test.

Next, we can estimate the value of the constant n. In Figure 2 the observed relationship between N_f and r are shown, accompanied by the curves representing the functional relation $r = 1 - n/N_f$ drawn when $n = 3, 4, 5$, and 6. We can see that the

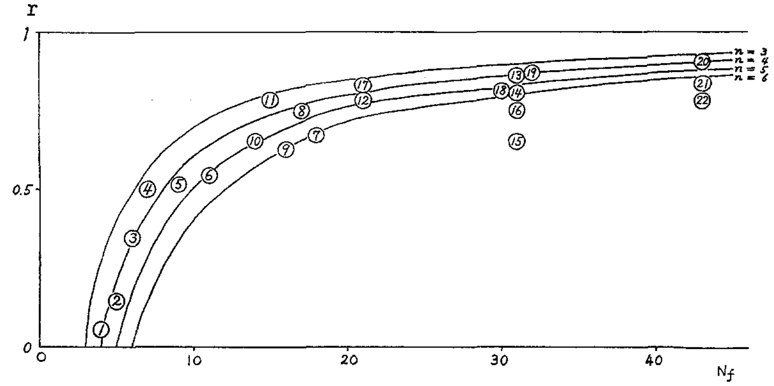

Fig. 2. The relationship between the number of adult females (N_f) (abscissa) and the common ratio (r) of the geometric sequence. Encircled point numbers 1–22 correspond to the troop numbers indicated in Table 1. The curves representing the functional relationship $r = 1 - n/N_f$, are drawn for $n=3$, 4, 5, and 6.

curve for $n = 5$ is best fitted to the observed relationship between N_f and r. This is supported by the fact that the mean of the n values calculated by the formula $n = N_f(1 - r)$ for each of the 22 data involved in the Table 1 is 5.3. Therefore, hereafter the functional relation,

$$r = 1 - \frac{5}{N_f} \tag{4}$$

will be used for our mathematical formulation.

Let us now assume that the genetic contribution of male parents to the next generation is proportional to their sexual activity. That is to say, assume that k_{mi} ($i = 1, 2, \ldots, N_m$) forms a geometric series with the common ratio r in lowering sexual rank. Because

$$\sum_i k_{mi} = k_{m1}\frac{r^{N_m} - 1}{r - 1} = N_c\,,$$

the genetic contribution of the first rank adult male (k_{m1}) is given as

$$k_{m1} = N_c \frac{r - 1}{r^{N_m} - 1}\,.$$

Because a new series, k^2_{m1}, k^2_{m2}, ..., is also a geometric series with the common ratio r^2, then

$$\begin{aligned}\sum k^2_{mi} &= k^2_{m1}\frac{r^{2N_m} - 1}{r^2 - 1} = N^2_c \frac{(r-1)^2}{(r^{N_m} - 1)^2}\,\frac{r^{2N_m} - 1}{r^2 - 1}\\ &= N^2_c\,\frac{1 - r}{1 + r}\,\frac{1 + r^{N_m}}{1 - r^{N_m}}\,.\end{aligned} \tag{5}$$

FORMULA FOR ESTIMATING THE EFFECTIVE TROOP SIZE

Substituting the relations (1), (3), and (5) for the four summations of the denominator of formula (2), and simplifying the formula, we obtain

$$N = \frac{4 - 2/N_c}{\dfrac{1 - r}{1 + r}\,\dfrac{1 + r^{N_m}}{1 - r^{N_m}} + \dfrac{1}{N_f} - \dfrac{1}{N_c}}\,.$$

Here, let us substitute the relation (4) for r in the above formula. Then,

$$N = \frac{4 - 2/N_c}{\dfrac{5/N_f}{2 - 5/N_f}\,\dfrac{1 + (1 - 5/N_f)^{N_m}}{1 - (1 - 5/N_f)^{N_m}} + \dfrac{1}{N_f} - \dfrac{1}{N_c}} \cdot \tag{6}$$

This can be considered as a formula for estimating the effective size of Japanese monkey troops. In this formula the variables are N_c, N_m, and N_f. By obtaining these values from the socio-ecological survey data involving social construction or age distribution of the troops, we can estimate the genetically effective size of the individual Japanese monkey troops.

RESULTS OF THE ESTIMATION OF THE EFFECTIVE SIZE OF JAPANESE MONKEY TROOPS

By using formula (6), let us estimate the effective size of Japanese monkey troops. The author collected 44 survey data of Japanese monkey troops involving clarification of their social construction or age distribution mainly from two Japanese primatological journals, *Primates* and *Yaen*. Table 2 gives the list of collection and the results of the estimation of the effective troop size. In the last column of the table the ratio N/N_c is presented in percentages for the individual troops. We can see from these results that the genetically effective size of Japanese monkey troops is ordinarily less than 40% of their apparent size or census number, excepting such cases in which an unnaturally high proportion of adult individuals are existing in the troop and so give remarkably higher percentages of the N/N_c ratio.

At the bottom of Table 2, totals for N_c, N_m, and N_f of those troops are shown. These total numbers disclose that

$$\left.\begin{aligned} N_m &= 0.2\,N_c \\ N_f &= 0.3\,N_c \end{aligned}\right\} \tag{7}$$

in average. Of course, we should consider the expression (7) as being of only a tentative nature, because (1) the troops which appear in the table can not be regarded as random samples of Japanese monkey troops, (2) the data involves replicated, therefore not independent, survey results of the same troop, and (3) the collection involves troops with a remarkably abnormal age distribution, as stated in the preceding paragraph. But, when we put the relation (7) in formula (6), we obtain a formula for estimating the effective troop size in which only one variable, (N_c), is involved, that is,

$$N = \frac{4 - 2/N_c}{\dfrac{5}{0.6\,N_c - 5}\,\dfrac{1 + (1 - 5/0.3\,N_c)^{0.2N_c}}{1 - (1 - 5/0.3\,N_c)^{0.2N_c}} + \dfrac{1}{0.3N_c} - \dfrac{1}{N_c}} \cdot \tag{8}$$

The results of the numerical calculation for this formula are given in Table 3, in which the values of N_c are set in a range from 10 to 2,000. From this table we can see that the N/N_c ratio has a limiting value below 36% when N_c is increasing. When only the data of census numbers are available in a Japanese monkey troop, we can obtain a rough estimate of its effective size by using Table 3. Furthermore, generally speaking, it can be said that the genetically effective size of a Japanese monkey troop, which has

Table 2. Results of the estimation of the effective size in various troops of Japanese monkeys.

Troop	Census Number (N_c)	Number of adult		Data cited from	Effective troop size (N)	N/N_c (%)
		Males (N_m)	Females (N_f)			
Koshima (Mar., 1953)	21	6	7	Tokuda (1961–2)	5.99	28.54
(Jan., 1957)	34	11	10	Tokuda (1961–2)	9.74	28.67
(Jan., 1958)	37	12	9	Tokuda (1961–2)	8.41	22.75
(Jan., 1959)	42	14	9	Tokuda (1961–2)	8.37	19.94
(Aug., 1962)	56	21	17	Tsumori et al. (1965)	18.55	33.14
(Nov., 1970)	122	30	30	Iwamoto (unpubl.)	34.10	27.95
Takasakiyama (May, 1953)	220	36	60	Sugiyama (1960)	67.00	30.45
(Jan., 1956)	370	51	110	Sugiyama (1960)	116.03	31.35
(Feb., 1959)	570	104	170	Sugiyama (1960)	195.38	34.27
Takasakiyama-A (Jan., 1960)	550	99	170	Sugiyama (1960)	193.72	35.22
(Dec., 1962)	517	71	154	Itani et al. (1963)	162.67	31.26
Takasakiyama-B (Jan., 1960)	100	20	24	Sugiyama (1960)	26.50	26.50
(Dec., 1962)	150	32	28	Itani et al. (1963)	31.28	20.85
Takasakiyama-Y (Dec., 1962)	73	17	14	Itani et al. (1963)	14.42	19.76
(Jan., 1963)	83	22	19	Kano (1964)	20.65	24.88
Minoo-B (Jan., 1956)	22	4	7	Kawamura & Kawai (1956)	5.91	26.90
(Aug., 1958)	29	2	11	Kawamura (1958)	6.55	22.60
Shodoshima-O (1957)	52	18	17	Yamada (1966)	18.62	35.82
Shodoshima-T (1957)	32	14	18	Yamada (1966)	20.83	65.09
Shodoshima-S (1957)	135	40	44	Yamada (1966)	52.06	38.57
Shodoshima-I (1957)	127	52	47	Yamada (1966)	56.99	44.87
Shodoshima-K (1957)	170	42	51	Yamada (1966)	59.84	35.20
Miyajima (Jan., 1970)	73	10	24	Hayashi (unpubl.)	23.48	32.17
Gagyusan (Dec., 1956)	135	15	45	Furuya (1963)	40.71	30.15
(Dec., 1957)	161	15	45	Furuya (1963)	40.24	24.99
(Mar., 1958)	119	10	33	Furuya (1963)	27.82	23.37
(May, 1962)	159	11	45	Furuya (1963)	33.48	21.05
Hieizan-B (Sept., 1964)	42	9	15	Hazama (1964)	15.58	37.11
Arashiyama (Dec., 1957)	65	16	20	Nakajima (1958)	22.00	33.85
(Mar., 1964)	155	25	50	Koyama (1967)	53.64	34.61
Takagoyama-I (Aug., 1964)	158	16	46	Nishida (1966)	42.16	26.68
Takagoyama-III (Aug., 1964)	110	12	46	Nishida (1966)	36.62	33.29
Hagachi-A (Sept., 1964)	72	12	23	Nishida (1966)	24.05	33.40
Takaosan (May, 1957)	50	16	16	Maeda (1963)	17.32	34.64
(Dec., 1962)	34	11	23	Maeda (1963)	25.64	75.43
(1967)	43	13	22	Maeda (1968)	24.75	57.56
Shirahama (Apr., 1952)	24	8	10	Tokuda (1959)	9.93	41.39
Shiga-A (Dec., 1962)	22	7	8	Suzuki & Wada (1964)	7.30	33.20
(Oct., 1963)	25	6	8	Suzuki (1965)	7.23	28.92
Shimokita-A (Mar., 1963)	15	3	5	Izawa & Nishida (1963)	3.41	22.74
Shimokita-O (Mar., 1963)	13	4	4	Izawa & Nishida (1963)	2.07	15.96
Shimokita-B (Mar., 1963)	8	3	4	Izawa & Nishida (1963)	2.15	26.93
Ohirayama (Feb., 1963)	58	21	37	Tsumori (1966)	44.32	76.42
Takeno Park (Dec., 1963)	45	8	18	Kawai (1964)	17.94	39.88
Total	5098	969	1573			

an average age distribution, is one-fourth to one-third of its apparent size or census number, that is, from the expression (7), a half to two-thirds of the total number of breeding males and females ($N_m + N_f$).

DISCUSSION

Several authors measured the effective size of *Drosophila* experimental population by different methods. Kerr and Wright (1954a, b) and Wright and Kerr (1954) estimated the average effective size from the steady process of changes in gene-frequency distribution of some mutant genes and obtained the values of 83% for the

Table 3. Results of numerical calculation of the formula (8).

Census number (Nc)	Effective size (N)	N/Nc (%)
10	0.28	2.87
20	4.68	23.43
30	8.39	27.99
40	12.01	30.04
50	15.60	31.21
75	24.52	32.69
100	33.41	33.41
150	51.16	34.10
200	68.90	34.45
300	104.36	34.78
500	175.27	35.05
1,000	352.53	35.25
1,500	529.79	35.31
2,000	707.05	35.35

forked gene, 72% for the Bar gene, and 67% for the spineless gene, relative to apparent size. BURI (1956) calculated it by a similar method from competition experiments between the two alleles of brown locus and obtained the values of 56% and 72% relative to apparent size. CROW and MORTON (1955) defined the index of variability in progeny number of parents and, by calculating this index from his experimental results on *Drosophila,* estimated an average effective size as 71–76% for female parents and 35–48% for male parents relative to apparent size. The author of the present paper (NOZAWA, 1963) estimated the effective size by measuring the random fluctuation of frequencies of a mutant gene in competition with its wild type allele, obtaining the ratio of effective (N) to apparent size (N') as 35–62% when $N'<10$ and 22–30% when $N'>10$. A more accurate estimation of effective size in relation to changes in parental population density was performed by the same author (NOZAWA, 1970). He showed that in a closed culture bottle environment the effective size enlarged along with the parental population density when the number of parental pairs was small, but the effective size came to be almost constant irrespective of the parental density when the number of parental pairs was above a certain level. Therefore, it was suggested that in the *Drosophila* mating population kept in a closed culture bottle the effective size had a certain maximum level which would be determined by the volume of the bottle, the area of culture media, and/or the amount of food for larvae.

In human populations CROW and MORTON (1955) tried to estimate an average effective size by measuring the index of variability in progeny number of parents mentioned above and obtained the value of about 70% as the ratio of effective size to apparent size. This means that CROW and MORTON recognized the ratio in human population to be about the same as in *Drosophila* experimental populations.

It is in the farm animal population that the effective size is extremely small in comparison with its apparent size. In a herd of farm animals, only a small number of elite males are used for reproduction and other males are culled or castrated and eliminated from the mating population, while almost all the females are ordinarily used for reproduction. In such circumstances, the sex-ratio in the reproductive population is used to deviate remarkably from one to one. According to the estimation of NOZAWA et al. (1962), the ratio of effective to apparent size was less than

10% in horse population in which insemination was made exclusively by natural copulation. On the other hand, in dairy cattle population of Japan where the artificial insemination (A.I.) technique is very much propagated, the ratio of effective to apparent size can be reduced almost infinitely by increasing the number of reproductive cows and the advancement of the A.I. technique (NOZAWA, 1964).

From the present work we find that the ratio of effective to apparent size in Japanese monkey troops has a level which is generally midway between the levels for human and farm animal populations. It can be considered that such circumstances are a genetic reflection of the sociological fact that the Japanese monkey troops are integrated by rank system among individual members in the troops.

Last of all, we should consider that the monkey populations have the property of overlapping generations, which would require some modifications to the mathematical formulation presented here. The author wishes to incorporate these circumstances into his theory by way of clarifying demographic parameters required for estimating the effective size of the monkey troops.

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Author's Address: KEN NOZAWA, *Department of Variation Research, Primate Research Institute, Kyoto University, Inuyama, Aichi, 484 Japan.*