

# Variations in the demographic structure and dynamics of gelada baboon populations

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Received October 31, 1983 / Accepted January 6, 1984

**Summary.** A comparative analysis of demographic variables for three populations of gelada baboons (*Theropithecus gelada*) showed that these were determined by a combination of environmental, demographic and social factors interacting in complex ways. Both birth rates and survivorship were found to be adversely influenced by the severity of local climatic conditions. These independently influenced adult sex ratio, which in turn determined the proportion of multimale reproductive units in the population. Mean harem size was found to be independent of all environmental and demographic factors with the sole exception of the proportion of harem-holding males, suggesting that it is mainly a consequence of social factors related to harem fission rates. Migration rates and band fission rates were related to population growth rates, these in turn being determined largely by local mortality and birth rates.

## Introduction

Demography, ecology and behaviour form a complexly interrelated system of variables (Altmann and Altmann 1979; Dunbar 1979). Attempts to investigate their systematic inter-relationships have been few, no doubt in part because their complexity demands large sample sizes if the individual relationships are to be teased apart. Nonetheless, such attempts are inevitable if we are to come to serious grips with complex biological systems.

In this paper, we use a comparative approach to explore some of the inter-relationships between

environmental and demographic variables in populations of gelada baboons. We will show that causal relationships, though complex, can be traced through a number of links, indicating that particular environmental variables can have widespread effects on both the demography and the behaviour of a population of animals.

## Materials and methods

The data are drawn from field studies of gelada baboons (*Theropithecus gelada*) in the Bole valley (Dunbar and Dunbar 1974) and the Sankaber and Gich areas of the Simen Mountains National Park (see Dunbar and Dunbar 1975 and Kawai 1979, respectively) in northern Ethiopia. Details of the study areas, populations, study periods and general methods are given by Iwamoto and Dunbar (1983). Most of the data quoted in this paper are based on study populations of 3 bands totalling 181 animals at Bole, 6 bands totalling 764 animals at Sankaber in 1971–1972, 4 bands totalling 559 animals at Sankaber in 1974–1975 and 3 bands totalling 303 animals at Gich. In addition, limited data are available from other bands in each of these study areas.

The three study areas covered the complete geographical, altitudinal, vegetational and climatic ranges of the species. Bole in the south was the lowest, warmest and driest, while Gich in the north was the highest, coldest and wettest. Fortuitously, rainfall correlated with altitude in the three study areas (a consequence in part of an east-west rain shadow effect). Rainfall is a good correlate of primary productivity (Rosenzweig 1968; Coe et al. 1976; Smith and LeCourt 1979), while ambient temperature is known to be a linear function of altitude. Detailed summaries of habitat and climatic variables for the three study areas can be found in Iwamoto and Dunbar (1983, Table 1).

Gelada baboons live in one male reproductive units (Crook 1966; Kawai et al. 1983). Each unit consists of a single breeding male and 1–10 reproductive females, together with their dependent offspring. Some reproductive units contain more than one adult male, though in these cases the extra males do not play a significant breeding role: these units are termed *multimale* units. Reproductive units associate together in higher level social groupings termed *bands*, with each of which are associated a small number of all-male groups of bachelor males.

Females are defined as being mature when they reach the normal age of first reproduction (4 years), but males are not

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considered to be adult until they cease skeletal growth at about 6 years of age when they are normally capable of holding a harem of breeding females for the first time (see Kawai et al. 1983). We distinguish between the number of animals of all ages and both sexes in each unit and the number of reproductive (i.e. post-puberty) females in the unit. The first will be termed *unit size*, the second *harem size*.

Kendall's correlation coefficient is used throughout this paper in order to permit the evaluation of partial correlations. We follow Kendall (1948) in using his correlation coefficient as a measure of association (or independence) in  $2 \times 2$  contingency tables. All significance levels quoted for statistical tests are 2-tailed.

## Results

In order to be able to generate causal explanations for phenomena, we adopt the strategy of testing between alternative hypotheses that might account for the observed distributions (cf. Iwamoto and Dunbar 1983). This allows us to determine the most likely causal explanation rather than having to resort to *ad hoc* speculation.

### Life-history variables

**Birth rate.** Birth rate was found to vary across habitats in such a way as to correlate with altitude (Table 1, top line). Figure 1 shows the same effect in terms of the numbers of immatures (less than 3.5 years old) per adult female in 10 bands at four different altitudes. Data from Debra Libanos at an altitude of 2,000 m are included here, based on Crook and Aldrich-Blake (1968). There is a significant negative correlation between the immature:female ratio and altitude ( $\tau = -0.778$ ,  $n = 10$ ;  $z = -3.13$ ,  $P = 0.002$ ).

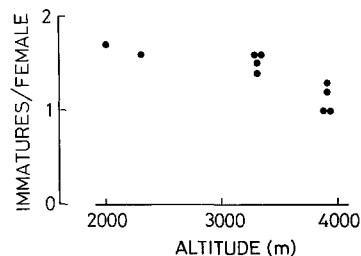
A number of factors can be identified that might be responsible for this effect: (i) temperature-stress may reduce birth rates as altitude increases because females have smaller energy surpluses to devote to reproduction; (ii) increasing food abundance (which is positively correlated with altitude) should result in increasing birth rates as rainfall increases because females will be able to achieve energy surpluses well in excess of metabolic requirements; (iii) birth rate may be expected to decline as group size increases due to competition among females (either for food or by giving rise to stress-induced ovulatory failure [cf. Dunbar 1980a and references therein]); (iv) birth rate may decline as sex ratio increases due to competition among females for access to males (cf. Dunbar and Sharman 1983).

Table 1 gives the relevant data to test between these hypotheses. The only hypothesis upheld by the data is temperature-stress, suggesting that this

**Table 1.** Tests of hypotheses to account for the variation in birth rate across habitats

	Bole	Sankaber		Gich	Fit to prediction
		1971	1974		
Birth rate/female/year	0.50	0.50	0.42	0.32	
<i>Hypotheses</i>					
1. Altitude (m)	2300	3300		3900	+
2. Annual rainfall (mm)	1100	1385		1467	-
3a. Band size (mean)	60.3	262	256	105	-
3b. Harem size (mean)	5.9	3.4	4.9	2.1	0
4. Adult sex ratio (females/male)	4.2 <sup>a</sup>	2.7	2.4	2.1	-

<sup>a</sup> Artificially high mortality of adult males in this area (see Dunbar 1977a)



**Fig. 1.** Number of immatures per adult female in individual bands plotted against the altitude of the study area

is the main factor determining variation in the birth rate in these populations.

We cannot determine from these data whether the differences in birth rate are due to differences in conception (or ovulation) rates or to differences in abortion rates. The first would imply that females are unable to ovulate due to an insufficiency of energy (or a specific nutrient) surplus to requirements (see Sadleir 1969; Jones and Ward 1976), while the second would imply that energy stress only becomes effective as the energy demands of the growing foetus become more severe. It seems unlikely that food shortage as such is implicated here: food availability in fact *increased* with altitude (see Iwamoto and Dunbar 1983), while Iwamoto (1979) was able to show that the Gich gelada were in energy surplus throughout the year at least as far as food availability was concerned. Evidence from Sankaber that birth rates correlate negatively with rainfall in any given year inclines us to favour the second explanation (see Dunbar 1980b). The lower birth rate at higher altitudes is thus more likely to be the result of generalised climatic stress

**Table 2.** Life history variables for the Simen populations

	Sankaber	Gich
Mortality rate ( $q_{i,i+1}$ ):		
0-18 months age	0.042	0.127
18-48 months age <sup>a</sup>	0.025	0.049
adult females	0.077	0.129
adult males	0.193	0.072
Survivorship to 48 months (females only)	0.878	0.800
Life expectancy (females): $e_0$ (years)	13.8	10.3

<sup>a</sup> Females only

and the consequent susceptibility to respiratory and related infections as altitude increases, such that females were more likely to lose fetuses through ill-health. This is supported by the finding that death rates at Sankaber are seasonally variable, being correlated with the amount of rainfall in any given period (Dunbar 1980b). Moreover, we show below that mortality rates among immatures increase with increasing altitude.

Nonetheless, it is still possible that nutritional stress might be implicated at a secondary level. For one thing, the protein content of the graze declined with altitude (Iwamoto and Dunbar 1983) and a dietary shortage of proteins or other nutrients would have severe effects on female reproductive rates even if the animals were in energy surplus. In addition, there is evidence to suggest that at the highest altitudes the gelada might be encountering time-budgeting problems such that, although there was an adequate *supply* of energy available, they may not have had sufficient time to harvest the quantities of energy required at critical times. Females might therefore find it difficult to sustain the high energy demands of gestation. Some evidence to support this hypothesis comes from the fact that the infant mortality rate during the period of lactation (first 18 months) is three times higher at Gich than it is at Sankaber, whereas once the infants are capable of fending for themselves the mortality rate at Gich is only twice that at Sankaber (see Table 2). Milk production is a relatively inefficient way of utilising energy and dietary shortage of protein is known to reduce milk production in ruminants (Maynard and Loosli 1969; Thorne et al. 1976).

In summary, it seems likely that the fall in birth rate as altitude increases is a consequence of temperature-stress, compounded by nutritional problems during critical periods of the reproductive cycle.

*Sex ratio at birth.* The sex ratio at birth was found to be exactly 1:1 at both Sankaber and Gich, although there was considerable variation within any given year due to small sample bias effects (see also Dunbar 1980b). Comparable data are not available for Bole. We conclude that sex ratio at birth is insensitive to variation in environmental conditions.

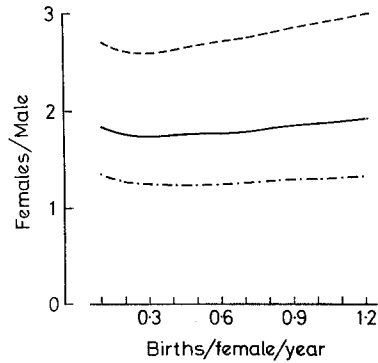
*Survivorship.* Data on various mortality and survivorship variables for Sankaber and Gich are given in Table 2. Following the recommendations of Caughley (1977), these were estimated directly from the mortality rates observed during study periods, not from the standing age distribution. Comparable data are again not available for Bole. It is apparent that the mortality rate among infants in their first 18 months of life is much higher at Gich than at Sankaber, a result that is in line with the difference in climatic stress experienced by the two populations. Similarly, mortality rates over the next 30 months of life are also higher at Gich (0.123/animal/year) than at Sankaber (0.063/animal/year), with a consequent lower survivorship to 48 months.

Mortality rates among adult females (>48 months of age) are also higher at Gich than at Sankaber, though the converse is true for males. The life expectancy for females is, as a result, higher at Sankaber than at Gich.

It seems most parsimonious to interpret the higher mortality rates at Gich as consequences of the more severe climate. This can probably be attributed to increased susceptibility to respiratory and other infections as the climate deteriorates, since, aside from parasitic infestations, these were found to be the main causes of death in both areas (Ohsawa 1979; Dunbar 1980b). Although the higher male mortality rate at Sankaber contradicts this hypothesis, we should be cautious about rejecting the hypothesis of climatic stress out of hand on the basis of this result alone. The higher male mortality rate might reflect the operation of other social and demographic processes (e.g. the higher rates of harem take-overs at Sankaber).

#### *Demographic structure*

*Adult sex ratio.* Table 1 indicated that adult sex ratio correlated positively with birth rate. The exceptionally high sex ratio at Bole should, however, be discounted since it reflects the fact that adult males are extensively shot by local tribesmen from time to time (see Dunbar 1977a). Nonetheless, for



**Fig. 2.** Results of a simulation to show the effect of birth rate on adult sex ratio in a non-declining population of animals with demographic parameters similar to those of the Simen gelada populations, using a Lesley matrix approach. The results are given for three different neonatal sex ratios, 60:40 males:females (*broken line*), 50:50 (*solid line*) and 40:60 (*pecked line*). The model assumes a constant birth rate for females of all ages greater than 4 years, an age-specific survivorship function similar to that observed at Sankaber (expectation of life at birth for males is  $e_0=11.5$  years, for females  $e_0=13.2$  years). Each simulation began with a standard population consisting of two animals in each year class (half males, half females) and was allowed to run until the adult sex ratio had stabilised. Females were considered to be adult at 4 years of age, males at 6 years. Birth rates greater than 0.3 per female yielded expanding populations, those below this value declining populations. Details of the simulation are given in the Appendix

the 3 Simen bands, there is a strong linear relationship between adult sex ratio and birth rate:

$$y = 1.028 + 3.320x \quad (1)$$

with  $r^2=0.996$ . The slope is significantly greater than 0 ( $t_1=15.59$ ,  $P<0.001$ ). The exceptionally high index of determination allows us some confidence in the validity of the relationship despite the paucity of data. Since we have already shown that the birth rate is determined by environmental factors and not by such demographic variables as sex ratio, we conclude that adult sex ratio appears to be a consequence of birth rate.

That this rather startling conclusion is not unreasonable can be shown by simulation. Figure 2 shows that, in expanding populations, the adult sex ratio becomes increasingly biased in favour of females as the birth rate increases, while the converse is true in declining populations (details of the simulation are given in the Appendix). The slope of this relationship becomes steeper as the neonatal sex ratio is biased increasingly towards females. Intuitively, it is not hard to see that this has to be so in a species that has a maturational lag, i.e. where females mature markedly earlier than males. In expanding populations, the females

entering the breeding cohort each year come from a more recent and hence larger birth cohort and have been subject to less mortality than the males entering the adult cohort that year, while the converse is true in declining populations.

An alternative explanation for these data might lie in differential mortality rates between the sexes. Adult male mortality rates were higher at Sankaber than at Gich, while the converse was true of adult female rates (see Table 2): this alone would tend to give rise to more even sex ratios at Gich than at Sankaber. We can show that this is so by re-running the simulation with female mortality rates identical to those for males. At a neonatal sex ratio of 1:1, the result was a reduction in the adult sex ratio corresponding to each birth rate, but the differences in the sex ratio between the two simulations was not constant: the slope for the new simulation was significantly steeper than that for the corresponding graph in Fig. 2 ( $t_{1,5} [b_1=0.632$  vs  $b_0=0.378] = 12.46$ ,  $P<0.001$ ).

Nonetheless, since the birth rate also varies between habitats, it is clear that both variables must be affecting the adult sex ratio. An analysis of variance of the results of the two simulations at an even neonatal sex ratio confirms that both contribute significantly to the variance in the observed values, though mortality rates clearly have a much greater influence than birth rates (birth rate,  $F_{9,9}=7.55$ ,  $P<0.01$ ; mortality rate,  $F_{1,9}=274.71$ ,  $P<0.001$ ). If we use the second simulation to estimate a value for Gich and determine values for the two Sankaber points from Fig. 2, we obtain a relationship for sex ratio regressed on birth rate of:

$$y = 0.664 + 2.411x \quad (2)$$

with  $r^2=0.821$ . Although the origin for Eq. (2) is rather lower than that for Eq. (1), the slopes of the two equations are not significantly different ( $t_1=4.27$ ,  $P>0.10$ ).

Thus, differences in adult sex ratio seem to be due to the combined effect of different natality and mortality rates.

*Structure of reproductive units.* Data on various aspects of the demographic structure of bands at Sankaber and Gich in different years are given in Table 3.

The mean number of females per harem (harem size) varied from 3.0 to 6.0 for the 18 bands in Simen. The mean harem size at Sankaber is not significantly different from that at Gich (Mann Whitney test,  $P>0.10$ ), but the mean size of reproductive units as a whole (all ages and sexes of animals) is significantly larger at Sankaber ( $P<0.05$ ).

**Table 3.** Demographic data for Simen bands

Band	Year	Band size	Number of		Adult sex ratio	Reproductive unit size ( $\bar{x}$ )	Harem size ( $\bar{x}$ )	Male harem-holders (%) <sup>b</sup>	Males in AMG <sup>a</sup> (%) <sup>b</sup>	Multi-male units (%)
			harems	AMGs <sup>a</sup>						
<i>Sankaber bands</i>										
Michibi	1971	211	20	2	3.0	9.6	3.7	80.0	8.0	15.0
Main	1971	262	25	3	2.7	10.0	3.4	81.3	6.3	23.1
Main	1974	256	17	2	2.4	14.7	4.9	48.6	20.0	35.3
Abyss	1971	79	6	1	2.7	12.7	4.5	60.0	10.0	33.3
Abyss	1974	123	11	1	2.3	11.2	3.7	61.1	5.6	36.4
High hill	1971	146	12	2	3.7	11.3	4.6	80.0	6.7	16.7
High hill	1974	163	12	3	2.8	12.3	4.7	60.0	25.0	16.7
E1	1971	30	3	—	1.8	7.3	3.0	60.0	0.0	66.7
E1	1974	69	5	1	2.5	13.0	5.4	45.5	9.1	60.0
E2	1971	36	2	1	2.4	13.5	6.0	40.0	20.0	100.0
E2	1974	71	5	—	4.0	14.2	4.8	83.3	0.0	20.0
<i>Gich bands</i>										
Gich	1971	112	11	2	2.7	9.7	3.7	73.3	13.3	18.2
Khadadit	1971	123	14	2	2.9	8.1	3.5	82.4	11.8	3.4
Khadadit	1973	170	18	1	2.8	9.2	3.1	66.7	16.7	11.1
Emetgogo	1973	106	10	1	1.6	10.4	3.9	38.1	42.8	40.0
Emetgogo	1975	105	11	1	2.1	9.9	3.5	56.5	16.7	30.9
Frekyo	1973	27	3	—	2.0	9.0	3.3	60.0	0.0	33.3

<sup>a</sup> All-male groups<sup>b</sup> Percent of all adult males

Dunbar and Dunbar (1975) reported a similar finding from a comparison of the sizes of individual units in two bands from each habitat, but interpreted this to mean that immatures had not been censused adequately during their much shorter study at Gich in 1971. In fact, the result is genuine, and, as can now be seen, is a consequence of the combination of a lower birth rate and a higher immature mortality rate at Gich. Harem size, however, is evidently not determined by habitat variables.

As an alternative, we might anticipate that the mean harem size might be a consequence of the adult sex ratio on the grounds that an increase in the number of females might simply be partitioned out among the same number of larger units. This turned out not to be the case ( $\tau=0.241$ ,  $z=1.35$ ,  $P>0.10$ ). The fact that mean harem size does not differ between habitats and is relatively constant despite considerable variance in adult sex ratio between bands rules out both ecological and demographic factors as likely explanations. In fact, social factors alone are probably responsible for reducing the natural variance in the size of harems by limiting the number of females who are prepared to remain together (see Dunbar 1980b, 1984).

*Band structure.* The proportion of multimale units does not differ significantly between the two study areas, nor does the proportion of males owning reproductive units (Mann Whitney tests,  $P>0.10$  in each case). Thus, any variation in the demographic structure of bands is likely to be a consequence of intrinsic demographic processes.

Acquisition of harems occurs through the entry of males from all-male groups into reproductive units, thereby giving rise to multimale units (see Dunbar and Dunbar 1974; Mori 1979). We therefore anticipate that many of the demographic variables will correlate with each other in predictable ways due to the effects of increasing competition as more males are excluded from reproduction through not being able to hold harems.

Mean harem size correlates only weakly with the percentage of adult males who are harem-holders (Kendall's  $\tau=0.265$ ,  $z=1.485$ ,  $P=0.136$ ), though the percentage of males in all-male groups is negatively correlated with the percentage of males that hold harems ( $\tau=-0.385$ ,  $z=2.157$ ,  $P=0.032$ ). We would expect the proportion of multimale units to be a function of the mean number of females per unit since, not only will the competition for units increase as the females are divided among fewer units, but large units are much easier

**Table 4.** Estimates of annual growth rates for 6 Simen bands

Band	Study area	Sample period	Gross annual growth rate <sup>a</sup>
Main	Sankaber	1971–1972	+16.2%
Main	Sankaber	1974–1975	+9.9%
Abyss	Sankaber	1971–1972	+14.7%
Abyss	Sankaber	1974–1975	+13.8%
Khadadit	Gich	1971–1973	+13.8%
Emetgogo	Gich	1973–1975	–0.3%

<sup>a</sup> Determined from initial population size with respect to the numbers of births and deaths recorded for the band during the study period. Migration into and out of each band has been discounted

for males to take over (Dunbar 1979, 1984). This prediction is not borne out by the data ( $\tau=0.157$ ,  $z=0.881$ ,  $P=0.378$ ). Nonetheless, the alternative expectation that the proportion of multimale units is negatively related to the percentage of harem-holding males is supported ( $\tau=-0.565$ ,  $z=-3.182$ ,  $P=0.002$ ), suggesting that the level of competition for units may be frequency-dependent. The level of competition, however, does appear to be independent of the actual distribution of harem sizes in the population, as is confirmed by an analysis of the partial correlations between mean harem size and the proportion of multimale units taking the correlation between harem size and the proportion of harem-holding males into account ( $\tau_{ab,c}=-0.008$  compared to  $\tau_{ab}=0.157$ ). In contrast, there is a very strong negative correlation between the proportion of harem-holding males and the adult sex ratio ( $\tau=-0.631$ ,  $z=3.535$ ,  $P<0.001$ ). This might be anticipated, for the more females there are per male in the population, the less competition there will be among males for units since, with harem size limited by social factors that relate exclusively to the females, there will be an increasing surfeit of females.

**Table 5.** Migration and band fission rates at Sankaber and Gich

Study area	Annual migration rate/animal		Annual migration rate/unit		Annual migration rate in units/animal		Annual fission rate per band		Net annual growth rate <sup>a</sup> (%)
	<i>P</i>	<i>n</i> <sup>b</sup>	<i>P</i>	<i>n</i> <sup>b</sup>	<i>P</i>	<i>n</i> <sup>b</sup>	<i>P</i>	<i>n</i> <sup>c</sup>	
Sankaber	0.019	597	0.027	48	0.024	597	0.125	16	5.2
Gich	0.013	306	0.036	31	0.007	306	0.111	9	6.2

<sup>a</sup> Mean annual population growth rate taking all sources of mortality and migration into account ( $n=4$  years at Sankaber,  $n=3$  years at Gich)

<sup>b</sup> Animal-years of data

<sup>c</sup> Band-years of data

## Demographic processes

**Population growth rate.** Estimates of the population growth rates per annum for 6 bands are given in Table 4. These are gross growth rates over the indicated periods, based on the numbers of births and deaths relative to the band size at the start of the period: migration has not been included. With the exception of the Emetgogo band at Gich, all rates are positive and of the same order of magnitude (overall mean = 13.7% per annum). For the three samples for which birth rate data are also available, there is a close correlation between annual growth rate and birth rate. In two of these cases, the mortality rates are also in complementary directions (mortality rates are not known in the third case), thus exacerbating the effects of birth rate on growth rate. The overall mean growth rate may be a little higher at Sankaber (13.7% per annum,  $n=4$ ) than at Gich (mean of 6.8% per annum,  $n=2$ ), again no doubt reflecting the milder climatic conditions at Sankaber. Note that the zero growth rate in the Gich Emetgogo band is consistent with the birth and death rates observed in 1973: the fecundity rate (i.e. female births per female) was 0.16 per annum while the female mortality rate was almost the same at 0.13 (Table 2). The Emetgogo band's ranging area was altitudinally the highest of all the bands in the sample and close to the altitudinal limit at which gelada can exist (see Iwamoto and Dunbar 1983).

**Migration rate.** Estimates of migration rates and band fission rates for Sankaber and Gich are given in Table 5. Comparable data are not available for Bole.

The migration rate for whole units (harems) are slightly higher at Gich than at Sankaber. However, the rate at which individuals migrated (both on their own and in reproductive units) is rather higher at Sankaber than at Gich. In fact, the gross

migration rate at Sankaber (0.043 per animal per year) was more than double that at Gich (0.020 per animal per year). This is in line with the greater growth rate of the Sankaber population (see above, Table 4).

Band fission rates tend to support this hypothesis, in that they are slightly higher at Sankaber than at Gich. However, the small sample size (16 band-years at Sankaber, 9 band-years at Gich) precludes any assessment of the statistical significance of the difference.

The exceptionally high population growth rates appear to be the consequence of a relatively benign habitat with a more than adequate food supply (see Dunbar 1977b; Iwamoto 1979). Nonetheless, in the long run, population *size* remained relatively stable even at Sankaber (Table 5; see also Dunbar 1978). This was mainly a consequence of the periodic migration out of the area of whole sections of a band following band fission. In two cases of band fission at Sankaber, 20–25% of the band moved out of the study area into a new home range. Such moves into new ranges could occur both upwards into the higher altitude zones and downwards into the arid lowlands at the base of the escarpment 1,500 m below. Both zones probably act as demographic sinks in which mortality rates balance or even exceed birth rates, with immigration from the more equitable intermediate zone being the main source of recruitment. As already noted, there is some suggestion that population growth rates decline with altitude, reaching zero net increase at an altitude of 3,900 m at Emetgogo (the highest point on the Gich plateau). It seems reasonable to suppose that at higher altitudes on the ridges to the south of Gich the growth rates would have been consistently negative. Iwamoto and Dunbar (1983) observed that gelada would begin to face serious time budget problems at altitudes only a few hundred metres higher than Emetgogo. The poor quality semi-arid lowlands at the foot of the escarpment would also impose severe energy and nutritional stresses on the animals, though in this case a combination of low food availability and dispersion with high ambient temperatures would be the main factors depressing population growth rates.

*Dynamics of band demography.* Table 6 gives for 6 bands the directions of changes in several characteristic demographic variables that occurred over the period 1971–1974 and for one band (the Emetgogo band at Gich) the changes that occurred during the period 1973–1975. These data can be used to check, on a dynamic intra-band basis, some of

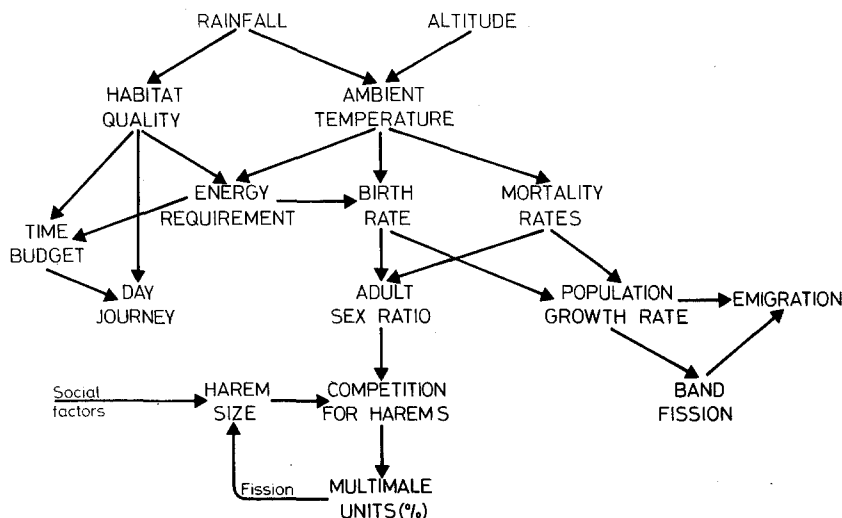
**Table 6.** Directions of changes in demographic structure of individual bands over time (based on data given in Table 3)

Band	Period	Sex ratio	Harem size ( $\bar{x}$ )	Male harem-holders (%)	Males in all-male groups (%)	Multimale units (%)
Main	1971-4	–	+	–	+	+
Abyss	1971-4	–	–	+	–	+
High hill	1971-4	–	+	–	+	=
E1	1971-4	+	+	–	+	–
E2	1971-4	+	–	+	–	–
Khad-adit	1971-3	=	+	–	+	+
Emetgogo	1973-5	+	–	+	–	–

the hypotheses derived from the preceding more static inter-band analyses of the data given in Table 3.

There are no consistent changes in any variable across bands. Irrespective of whether the data for the Emetgogo band are included or not, none of the distributions differ significantly from a random distribution (sign tests,  $P \geq 0.7$ ). This lack of synchrony between bands, many of whose ranging areas overlapped, implies that internal changes in band demographic structure are not determined by generalised environmental factors such as rainfall or temperature that have widespread effects. Rather, it seems more likely that the dynamics of individual bands are internally driven by demographic processes specific to each band, and that these processes behave independently from one band to another within the constraints imposed by the general environmental conditions.

The intercorrelations in Table 6 reveal strong negative relationships between changes in the proportion of multimale units and the adult sex ratio and between changes in the proportion of harem-holders and the proportion of males in all-male groups ( $\tau = -1.00$ ,  $n = 7$ ,  $P < 0.001$  in each case). These results support those derived above from the more static comparative analysis of band structure by showing that, when one variable is changed, the other changes in the predicted direction. Interestingly, there is also a strong negative relationship between changes in mean harem size and the proportion of harem-holding males ( $\tau = -1.00$ ,  $n = 7$ ,  $P < 0.001$ ), even though there is only a weak partial correlation between these variables in the inter-band analyses of Table 3. This is probably a consequence of the fact that the relationship between the two variables is a weak one:



**Fig. 3.** Flow diagram of the causal network in the gelada socio-ecological system, based on the results given in this paper and by Iwamoto and Dunbar (1983)

consequently, while the directions of any changes that occur are correlated, the magnitudes of the changes are not monotonically related in any strictly deterministic sense.

### Discussion

Iwamoto and Dunbar (1983) were able to show that environmental conditions (in particular the severity of the climate) directly influenced a number of aspects of gelada behavioural ecology. As a result of temperature stress, higher energy intakes are required to maintain body temperature as altitude increases, which in turn required a greater proportion of the activity budget to be devoted to feeding. If effects of this kind are severe enough, they can be expected to have repercussions for both mortality and birth rates.

In this paper, we have demonstrated just these effects, though whether these effects are mediated directly by energy stress or by susceptibility to disease is open to debate. Iwamoto's (1979) analysis of energy consumption and our own conclusions on the causes of mortality tend to favour the second explanation, though it remains possible that energy stress may be the ultimate cause. Of rather more interest, however, is the fact that we have been able to pursue the causal chain several steps further by demonstrating that these effects (birth rates) influence other demographic variables (notably adult sex ratio), which in turn have further repercussions with profound behavioural and reproductive consequences (i.e. by determining the proportion of males who hold harems, this in turn determining the proportion of multimale units in the population). These relationships are summarised in Fig. 3.

Multimale units are the combined products of the entry of follower males into reproductive units and of take-over fights (see Dunbar and Dunbar 1974; Mori 1979). Their frequency in the population reflects the frequency with which the males in the population pursue these strategies of harem acquisition during any given period. As may be expected, this variable correlates with the proportion of adult males who are members of all-male groups, suggesting that the frequency of harem entry is a consequence of the degree of competition for reproductive units. While mean harem size does not correlate well with any of the environmental and demographic variables considered here, there is some suggestion of a weak relationship with the proportion of multimale units. This is to be expected, since only multimale units can undergo fission, and this is the main process balancing the natural growth rate of units (females mature into their natal units and do not otherwise leave: see Ohsawa 1979; Dunbar 1980b). The weakness of this relationship can probably be attributed to the fact that the additional males of multimale units are the products of two rather different processes of harem acquisition (take-overs and follower-entry), but that it is only as a result of one of them (follower-entry) that units generally undergo fission.

That particular demographic variables can have widespread consequences for both the demographic and social aspects of a species' biology is very seldom appreciated (see Dunbar 1979; Altmann and Altmann 1979), partly no doubt because field workers are usually restricted to studying a single group at a particular moment in time. Yet, it is clear from the present results that demographic variables can respond in quite dramatic ways both



to environmental factors and to the influence of other demographic variables. As more data become available, both from long term studies and from more studies of the same species in different habitats, it is becoming increasingly clear that demographic structure and life-history variables are not immutable species-specific parameters (see also Dunbar and Sharman 1983). Consequently, to the extent that behaviour is subject to demographic influence, so the consideration of demographic variables as an integral component of the biological system becomes increasingly necessary.

## Appendix

### Outline of computer program for the demographic simulation

The simulation determines, by an iterative procedure analogous to a Lesley matrix approach, the effects on the future adult sex ratio of changes in the birth rate in a population with a maturational lag and life-history characteristics similar to those of the Sankaber gelada. The simulation began with a standard population consisting of one male and one female in each of 17 and 20 year-classes, respectively. The simulation ran for 50 cycles (years) to allow time for the adult sex ratio to stabilise (this usually occurred within 20–25 cycles). The simulations were run for three different values of the neonatal sex ratio in order to determine how the adult sex ratio is affected by variation in this variable. The ratios used were 60:40, 50:50 and 40:60 males:females, respectively.

The program outline was as follows:

1. For each run, set the fecundity rate to each value between 0.05 and 0.70 female-births per female per year (using an interval of 0.05). Note the difference between the fecundity rate (the number of *females* born to each female) and the birth rate (the numbers of offspring of *both sexes* born to each female);

2. Calculate for each year  $i$ :

- (i) the number of breeding females (by summing the number of females in year classes 4–20 inclusive),
- (ii) the number of offspring born (from [2.i] using [1]);

3. For each sex, adjust the numbers of animals in the  $i + 1$ th sex-year class by devaluing the number in the  $i$ th class by the age/sex-specific mortality rate (see below);

4. Set the number of males and females in the first year class equal to [2.ii];

5. Calculate the adult sex ratio by:

- (i) summing the number of females in year classes 4–20 inclusive,
- (ii) summing the number of males in year classes 6–17 inclusive,
- (iii) dividing [5.i] by [5.ii];

6. Repeat from [2] for the next year until year 50;

7. Plot adult sex ratio in year 50 (from [5.iii]) against the birth rate (from [1]);

8. Repeat from [1] for the next fecundity rate.

The equations for the age-specific survival rates were obtained by fitting linear regressions to the data given by Dunbar (1980b, Table 10) and were as follows:

For females,

$$\begin{aligned} i < 6, & & q_i &= 0.9580 + 0.0066i \\ 5 < i < 17, & & q_i &= 1.1082 - 0.0186i \\ 16 < i < 21, & & q_i &= 2.9810 - 0.1355i \\ 20 < i, & & q_i &= 0 \end{aligned}$$

For males,

$$\begin{aligned} i < 6, & & q_i &= 0.9580 + 0.0066i \\ 5 < i < 12, & & q_i &= 1.0904 - 0.0245i \\ 11 < i < 18, & & q_i &= 3.1606 - 0.1892i \\ 17 < i, & & q_i &= 0 \end{aligned}$$

*Acknowledgements.* The field work was made possible by grants from (1) the Ministry of Education, Japan, and (2) the Science and Engineering Research Council, U.K., and the Wenner-Gren Foundation for Anthropological Research, respectively. We are grateful to the Ethiopian Government Wildlife Conservation Organisation for permission to work in the Simen Mountains National Park and to the park wardens for their cooperation and support. RD is also grateful to the Bole Valley Society for permission to work at Bole. We are greatly indebted to our colleagues, Professor M. Kawai, Drs T. Iwamoto and U. Mori and Patsy Dunbar for their assistance in the field. This paper was prepared for publication while RD was in receipt of an SERC Advanced Research Fellowship; its completion was greatly facilitated by a Travel Fellowship awarded to RD by the Japan Society for the Promotion of Science and by Professor M. Kawai's hospitality while RD was a visitor at the Primate Research Institute, Inuyama.

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