Intrinsic Rate of Natural Increase among the Pahira

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Fitness in the Darwinian sense is defined in terms of the ability of an individual or of a population to leave behind progeny. The greater the number of progeny one leaves behind, the higher one's fitness to the particular environmental niche inhabited. Fitness defined in this manner is therefore a function of the fertility and mortality patterns a population experiences at a given point in time. The best single measure of fitness is considered to be the intrinsic rate of natural increase, r, which measures the capacity of a population to grow under the existing patterns of fertility and mortality, assuming a stable population with an unchanging age structure determined solely by its stable fertility and mortality schedules and without in- or out-migration.

The importance in genetics of this population parameter, r, was appreciated fairly early (Fisher, 1930), but it has only recently begun to be applied by human population geneticists (Roberts, 1968). Data from only a limited number of populations are thus far available. Comparative data from populations in different socioeconomic levels are urgently needed, in order to assess their relative potentialities for survival and contribution to the genetic makeup of the future population of a specified area, as well as of the species as a whole.

Demographic information was collected from the Pahira, a food-gathering tribal community of eastern India, as part of a population genetical survey of this community, beginning early 1963. The Northern Pahira inhabit the foothills and slopes of the Ajodhya hills in Purulia District, West Bengal, and the two groups of Southern Pahira, those of the Dalma hills and the ranges beyond the Subarnarekha river, live in Singhbhun and Ranchi districts, Bihar. A detailed report on the results of our survey has been presented elsewhere (Basu, 1969) and provides information we have not been able to include in this brief report. Subsequently, the data were further analyzed to calculate the intrinsic rate of natural increase, by sex, separately for the three partially endogamous subgroups of the Pahira—the Northern Pahira, Southern Pahira I, and Southern Pahira II. The values of r obtained are presented here not only to provide data but also to demonstrate that this parameter can be estimated for unsophisticated populations like the Pahira for which life tables or birth and death registration data are not available, from the kind of information obtainable by intensive surveys.

MATERIALS AND METHODS

Extensive genealogies were collected covering the entire Pahira population. The information collected on every living individual was name, age, sex, residence, birth place, marital condition, and position in an extended genealogy. In addition, for adults, information on children ever born, in order of birth, sex and age or age at death of children, age at death of spouses (whenever possible) in case of widows or widowers, sibs by age or age at death and in order of birth (as far as the informant could remember) was collected.

The method followed in calculating r was essentially that of Birch (1948) as described by Roberts (1968) and the data are presented in Table 1. However, the proportion surviving to a given age (l_x) and the mean number of offspring produced per person during a given 5-year age period (m_x) could not be calculated directly in the absence of reliable records either of age at death for most of those who died after adulthood or age of mothers at birth of the children who subsequently died. The difficulties were circumvented in the following ways.

Fairly reliable information on age at death of children could be obtained from the mothers. Taking elderly mothers only (where the youngest child was around 20 years of age), the number of offspring ever born and the number dying in 0–4, 5–9, 10–14, 15–19 age groups were counted. From these numbers, proportion surviving up to age x were calculated up to l_{20} (l_5 = all births − deaths 0–4 / all births). If we consider the fact that some women in the population died young (for instance, during or immediately after birth of the first child) and their children died with them (due to lack of maternal care), inclusion of these women in our sample would have increased

our estimate of mortality and decreased that of survival. In other words, the estimate of mortality obtained from our sample which comprises living elderly (50+) women only probably underestimates the true mortality and overestimates the true probability of survival. Since some of the children born to these women were around 20 at the time of this investigation and therefore had not lived long enough to die after 20, estimation of l_{25} and over from these data did not seem useful.

A small number of "adult sibships" (comprising adult sibs, where information was collected from the sibs and not from their parents who were long dead) in which the ages at death of adult sibs were available from the surviving ones or from the spouses of the dead ones was used to calculate l_{20} and over. It was assumed that the total number of individuals in these "adult sibships" represented survivors over age 15, i.e., these adults remembered those of their sibs who survived to age 15 or over. This assumption is based on the fact that the earliest age at death of sibs mentioned by surviving adults is in the period 15–19. By equating this number to the proportion surviving to age 15 (as obtained from the

TABLE 1

DATA USED IN THE CALCULATION OF r FOR THE PAHIRA

Age Interval and Net Production Rate	Pivotal Age (x)	Prob. of Survival to Age x (l_x)*	Mean Fert. of Individ. in Each Age Interval (m_x)*	$\frac{1}{2} l_x m_x$	$4-rx$ $(r=0.0119)$	e^{4-rx}	$(e^{4-rx} (\frac{1}{2} l_x m_x)$
10–14	12.5	0.697	0.071	0.025	3.851	47.040	1.179
15–19	17.5	0.666	0.548	0.182	3.792	44.345	8.071
20–24	22.5	0.606	0.850	0.258	3.732	41.763	10.775
25–29	27.5	0.563	1.200	0.338	3.673	39.370	13.307
30–34	32.5	0.520	1.111	0.289	3.613	37.077	10.715
35–39	37.5	0.477	0.833	0.199	3.554	34.953	6.956
40–44	42.5	0.434	0.500	0.109	3.494	32.917	3.588
Net reproduction rate	. . .	. . .	. . .	1.400	. . .	. . .	54.588

* See text for method of calculating the $l_x m_x$ values.

"young sibships") and projecting backward, the total number of births in the "adult sibships" was estimated.

From the estimated total number of births and the reported number of survivors to age x ($x = 20, 25, \ldots$) in the "adult sibships," calculation of the proportion surviving to age x was straightforward. Finally, l_x values for "young" and "adult" sibships were put together. The assumption involved in putting together the l_x values for the "young" and "adult" sibships is that the mortality pattern has not changed over the years. The same assumption is involved in pooling together different cohorts in the "young sibships" as in the "adult sibships." The assumption does not seem unrealistic since the way of life does not seem to have changed to any considerable extent in this population on which the effects of overall modernization in the country have hardly, if at all, made any impact.

The pedigrees used to calculate the m_x values were those in which the mothers, as well as all the offspring ever born to them, were alive at the time of this investigation (so that the age of mothers at birth of each child could be calculated from the difference between the mother's and the child's age), and those in which the dead offspring was between two surviving ones so that the mother's age group at the birth of the dead child could be estimated (e.g., if two surviving children were born at mother's age 20 and 25, then the dead one born in-between must have been born in the age period 20–24).

These pedigrees were only a part of all the pedigrees collected. For the pedigrees in which the mothers lost many of the children born to them, age of the mother at birth of each child could not be guessed and therefore such pedigrees were excluded from this analysis. The assumption implied in using such m_x values obtained from the kind of pedigrees described above as representative of the population is that there is no remark-able variation in fertility between the mothers who have lost many offspring and those who have not. Further, the fact that some of the mothers were still in their reproductive period at the time of our investigation and were expected to produce more offspring implies that the m_x values obtained were underestimates of the true values, but probably the differences were not large. Finally, several cohorts were pooled in calculating the m_x values, on the assumption that the fertility pattern had not changed over the years.

The calculations of the l_x values were based on all pedigrees with mothers aged 50 or above and all reliable "adult sibships." The m_x values were obtained from all pedigrees in which the mother's age at birth of all children could be assessed. However, these pedigrees do not include all the pedigrees at our disposal since some pedigrees lacking the desired information had to be excluded. Therefore, the estimates are subject to sampling variance and will have to be viewed with caution.

Once the l_x and m_x values were obtained, the $\frac{1}{2} l_x m_x$ figures were computed. The m_x values were halved on the assumption that half of the total offspring born in a given period were male and half female. The value of r was obtained by iteration, trying out different values of r until the column (e^{4-rx}) ($\frac{1}{2} l_x m_x$) added up approximately to 54.5982 (i.e., e^4). The choice of e^4 did not have any special significance; other powers of e (e^7, e^6, etc.) could be used instead.

The same procedure was followed for calculating r for the male samples.

<div style="text-align:center">RESULTS</div>

The results of our computation of r are given in Table 2.

The r_{female} values show that the Northern Pahira (N.P.) may be precarious but the Southern Pahira (S.P.) I and II are slightly better off. In genetic terms, considering females only, the N.P. gene pool is

TABLE 2

VALUES OF (r) BY SEX FOR THE
THREE PAHIRA SUBGROUPS

Subgroup	Male	Female
North Pahira......	+0.0100	−0.0028
South Pahira I....	+0.0052	+0.0119
South Pahira II...	+0.0121	+0.0131

relatively unfit, the S.P. I more fit and the
S.P. II the fittest of all the three subgroups.
In general, this seems to be due to the in-
creasing probability of leaving viable female
offspring (considering the $\frac{1}{2} l_x m_x$ column in
Table 1) from the N.P., through the S.P. I,
to the S.P. II. We do not have any medical
data on the relative prevalence of the differ-
ent diseases affecting fertility and mortality
in the three subgroups, and therefore, the
selective forces responsible for the observed
fitness differentials cannot be conjectured.
However, it is worth pointing out that the
impression obtained from the r_{female} values
agrees with that obtained from our compu-
tation of the index of total selection inten-
sity, I, (Crow, 1958), presented elsewhere
(Basu, 1967): 1.133, 0.738, and 0.687 in the
N.P., S.P. I and S.P. II, respectively. The
reliability of both results seems increased by
agreement between the impressions given by
the r and the I values, which were calculated
from the same kind of information, i.e., fer-
tility and mortality, but on the basis of
somewhat different samples (for I most of
the pedigrees available were utilized, where-
as for r only a small part of them were used).
If this trend of increasing capacity for
growth from the N.P., to the S.P. I and the
S.P. II, in that order, has continued for a
fairly long time, it may explain the differ-
ence in the population sizes (N.P., 301; S.P.
I, 475; S.P. II, 577) of the three subgroups;
if it should continue in the future, the S.P.
II component of the Pahira population as a
whole will gradually increase, with the re-
sult that the gene frequency of the Pahira

as a whole for any given locus will change
gradually in the direction of the S.P. II gene
frequency of that locus. This may be an im-
portant mechanism of microdifferentiation
of a population in the time-scale, not neces-
sarily involving selective advantage or dis-
advantage of specific alleles, but merely as a
function of differential growth potentials of
its constituent subgroups. Similar analyses
of other subdivided populations are neces-
sary in order to assess the importance of this
mechanism for human microevolution in
general.

The r_{male} values differ from those of the
females. The male values are all positive,
and while the S.P. II has the highest value,
as in the female, the lowest value occurs in
the S.P. I rather than in the N.P. The in-
creasing capacity for growth from the N.P.
to the S.P. I and S.P. II, in that order, is not
apparent in the case of males. The sex differ-
ence is relatively slight in the case of the
S.P. II, but is more marked in the N.P. and
S.P. I. The r value is lower for males than
females in the S.P. I and S.P. II, but higher
in the N.P.

We do not offer any interpretation of the
sex difference. Small sample size leading to
high sampling variance of the estimate is a
possibility. Alternatively, the m_x values for
males might have been underestimated.
When the information on children ever born
to a male was collected from the father
(when the mother was dead) fewer of those
children who died shortly after birth might
have been mentioned than when the infor-
mation was collected from the women since
men tend to forget about these children
more than women do. This explanation does
not apply to the N.P., unless we assume that
in this case the women were more forgetful,
which seems to be unrealistic.

Another explanation may be the rela-
tively lower fertility of males in the S.P. I
and S.P. II, not in the N.P. This explana-
tion is suggested by the m_x columns and the
net reproduction rates and a remarkably

higher probability of survival for the males in the N.P. compared to the smaller and inconsistent pattern of sexual difference in the I_x values in the S.P. I and S.P. II. The relatively lower fertility of the males may be explained under the assumption that given the prevailing social situation it is virtually impossible for a woman to live singly for any considerable length of time and support herself, but this is not true for a man. Thus, a woman is constantly exposed to the chance of reproduction while a man is not. Apparently this explanation does not apply to the N.P. situation. The probability of an individual to marry more than once cannot be related to the individual's fertility because in all three subgroups men have a higher probability of marrying more than once than females (Basu, 1969).

As a final comment, comparing the r values above with the r value of 0.0190 for India as a whole during 1951–61, it appears that while all but the N.P. female value suggest a moderate rate of growth for the Pahiras, the rates are lower than that of the country as a whole. It seems that the Pahiras are not partaking in the "explosive" population growth in India.

SUMMARY

The intrinsic rate of natural increase, r, has been calculated for the Pahira, a food-gathering tribe of eastern India, to indicate that this parameter can be at least tentatively estimated for an unsophisticated population. The method of computation and the assumptions involved have been described, and the results are discussed in the light of their probable implications.

REFERENCES

BASU, A. 1967. Selection intensities in the Pahiras. Eugen. Quart. 14:241–242.
———. 1969. The Pahira: A population genetical study. Amer. J. Phys. Anthrop. 31:399–416.
BIRCH, L. C. 1948. The intrinsic rate of natural increase of an insect population. J. Animal Ecol. 17:15–26.

CROW, J. F. 1958. Some possibilities for measuring selection intensities in man. Hum. Biol. 30:1–13.
FISHER, R. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.
ROBERTS, D. F. 1968. Genetic fitness in a colonizing human population. Hum. Biol. 40:494–507.