Supporting information for Journal of Evolutionary Biology article *Natural selection. VII. History and interpretation of kin selection theory* by Steven A. Frank

File: WDH_notes_part2_SuppInfo.pdf in PDF format

Contents: Notes written and distributed by William D. Hamilton for his graduate course at the University of Michigan, Fall 1979. Class attended by Steven A. Frank. Notes scanned by Frank in October 2012.

Comments by Steven A. Frank: These notes are a class assignment given my Hamilton to test students' understanding of group selection. The answers to the questions and some general comments on group selection are given on the final two pages.

Artificial data used to illustrate the evaluation of two levels of selection, i.e. selection within and between groups

1. Figures in the accompanying table represent fitnesses in a population consisting of five groups. Reproduction is parthenogenetic, generations are non-overlapping: individuals are of two genetic types, g and G.

Complete the table.

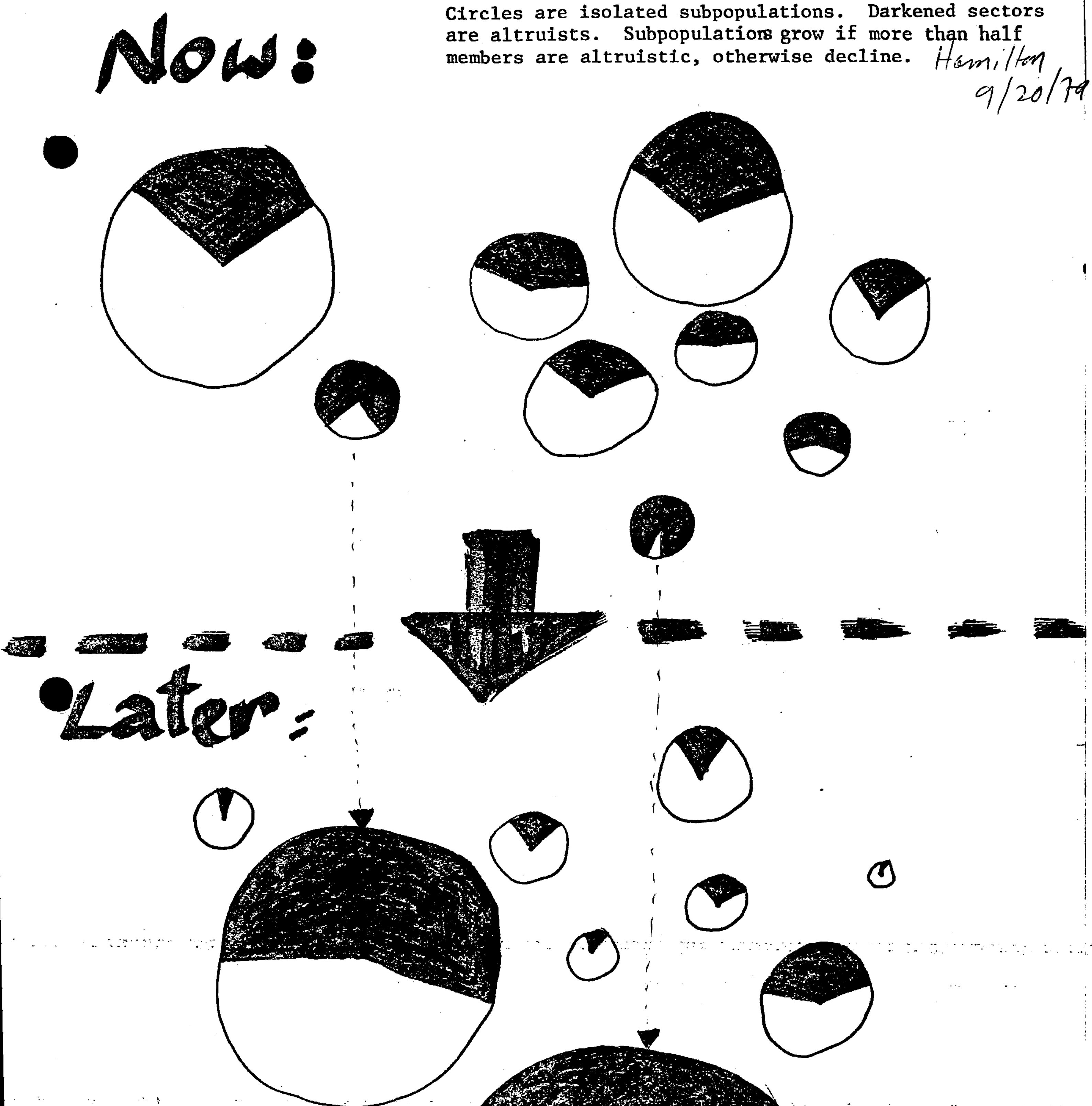
2. Using results calculated in the table, show the overall gain of G in the current generation due to selection ($w\Delta q$), and show this analyzed into two components, representing the partial gains due to selection within groups and due to selection between groups.

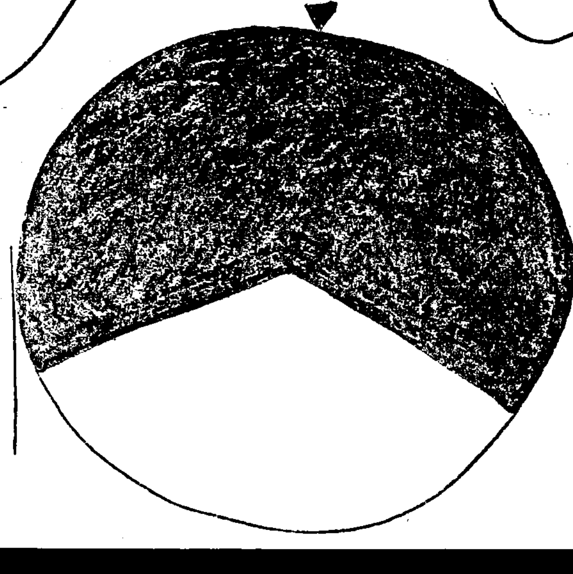
3. What kind of social behavior by g seems to be revealed by this data?

4. What does the distribution of group compositions suggest about the way groups are formed? (Hint: contrast to a binomial distribution).

5. If fitnesses continue to depend on genotype and group composition roughly as indicated in the data above, over a series of generations, would you expect fixation or equilibrium eventually? (In considering this question it may be assumed that groups 2, 3 and 4 actually consist of several groups of similar composition that have been lumped together).

Circles are isolated subpopulations. Darkened sectors are altruists. Subpopulations grow if more than half members are altruistic, otherwise decline. Hamilton 9/20/79





oth number of altruists and
equency of altruists have increased--
hanks mainly to two populations.

ut what will happen over later
quivalent time intervals? And how
ould original situation have been
et up? Founders (Colonizers).

		Fitnesses	Means	w_s	β_s	q_s	$p_s q_s$	$Cov(w_{si}, q_{si})$	n_s	$q_s - q$	$w_s(q_s - q)$
Group 1	g	0, 1, 1, 2,									
	G	none									
Group 2	g	3, 3, 4, 5, 5, 6									
	G	2, 4									
Group 3	g	4, 5, 5, 7, 8, 8, 9, 10									
	G	4, 4, 4, 4, 5, 6, 6, 7									
Group 4	g	7, 9									
	G	4, 6, 7, 7, 8, 8									
Group 5	g	none									
	G	7, 7, 7, 7									
						Weighted mean:			Weighted mean:		
Whole population	g										
	G										

$\beta_s \times p_s q_s$

		Fitnesses	Means	w_s	β_s	q_s	$p_s q_s$	$Cov(w_{si}, q_{si})$	n_s	$q_s - q$	$w_s(q_s - q)$
Group 1	g	0, 1, 1, 2,	1	1	-	0	0	0	4	$-\frac{1}{2}$	$-\frac{1}{2}$
	G	none	-								
Group 2	g	3, 3, 4, 5, 5, 6	$4\frac{1}{3}$	4	$-\frac{4}{3}$	$\frac{1}{4}$	$\frac{3}{16}$	$-\frac{1}{4}$	8	$-\frac{1}{4}$	-1
	G	2, 4	3								
Group 3	g	4, 5, 5, 7, 8, 8, 9, 10	7	6	-2	$\frac{1}{2}$	$\frac{1}{4}$	$-\frac{1}{2}$	16	0	0
	G	4, 4, 4, 4, 5, 6, 6, 7	5								
Group 4	g	7, 9	8	7	$-\frac{4}{3}$	$\frac{3}{4}$	$\frac{3}{16}$	$-\frac{1}{4}$	8	$\frac{1}{4}$	$\frac{7}{4}$
	G	4, 6, 7, 7, 8, 8	$6\frac{2}{3}$								
Group 5	g	none	-	7	-	1	0	0	4	$\frac{1}{2}$	$\frac{7}{2}$
	G	7, 7, 7, 7	7								
							Weighted mean: - .30			Weighted mean: + .45	
Whole population	g		5.1	5.4	.6	.5	.25	.15	40		
	G		5.7								

Gain of G between groups : .45
" " " within " : -.30

Total gain of G : .15

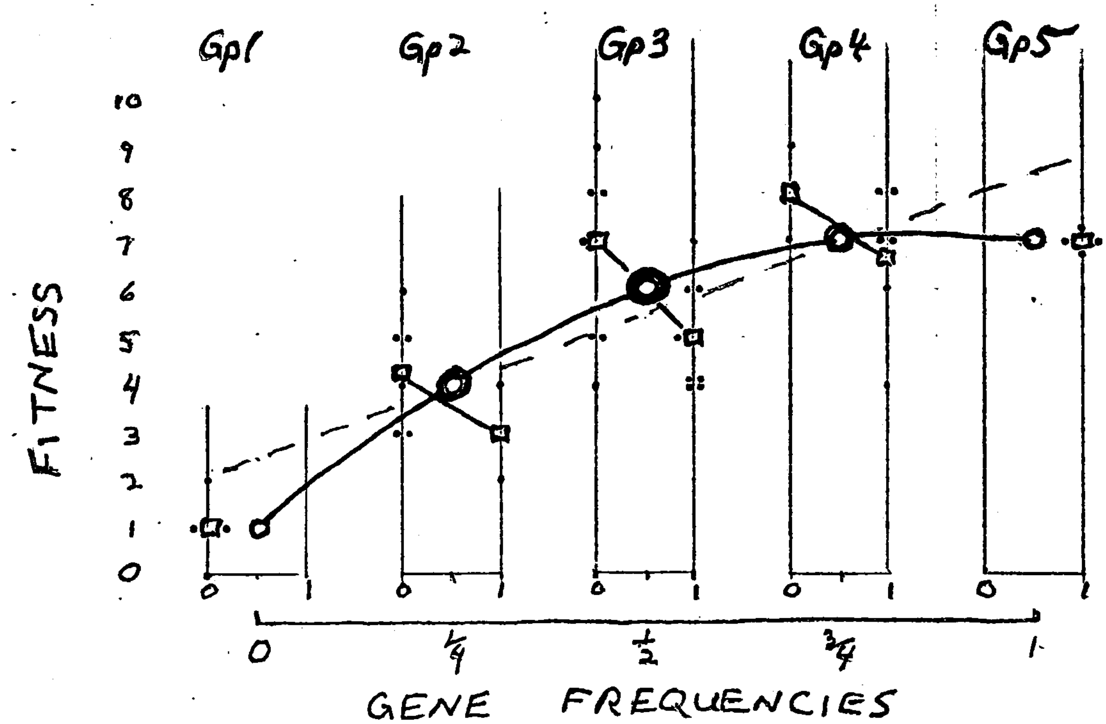
Answers and notes on the group selection example

1.& 2. A correctly completed table is set out on accompanying sheet.

3. G causes altruistic behavior. In every group it reproduces less, on average, than g, but groups which have more G's have higher mean fitnesses than groups with fewer.

4. (The hint for Q5 should also have been given as a hint for Q4). The answer is that it looks as if groups may be formed by some process of chance assortment from a pool but with a moderate tendency for like types to group together.
Once it is seen that groups 2,3, and ~~3~~ 4 may be composites of basic groupings of 4, containing 2,4 and 2 of such basic groups respectively, the overall distribution 1, 2, 4, 2, 1 can be considered and compared to the binomial as suggested. The distribution is symmetrical and so the 5-class binomial distribution to which it might be compared is 1,4, 6,4,1. Even without reducing this to an equivalent total of 10 it can be seen that this distribution is more centrally concentrated. Since the binomial is what would result if groupings had been made up wholly at random, the more spread-out distribution given indicates that there is some tendency for like genotypes to associate.
This means that the between group variance is greater than if grouping had been random (when its expectation would have been $\frac{pq}{n} = \frac{\frac{1}{2}\cdot\frac{1}{2}}{4} = \frac{1}{16}$).
This is favourable to the altruistic type G.

5. Here the following composite sketch of regressions within and between groups, drawn from data obtained in the table, may be useful:



Here dots show the individual fitnesses, squares show mean fitnesses of types within groups.
It is more instructive to connect the mean fitnesses of groups with a

curved line than to calculate and put in the linear regression line for the group means (although I have put this in lightly dashed,for interest) whenever a fairly obvious curved trend is shown.
The curvature indicates that the benefits from altruism tend to saturate, i.e., it hardly helps a group to have more than half its members altruistic, whereas having a few versus none made a large difference.

If the frequency of altruists increases (as our calculation shows that it does -- somewhat slowly), and in each generation groups are re-formed on roughly the same quasi-random principle that gave the currently observed grouping, then the diagram for the next generation is expected to be much the same except that the weighting of the circles will be more to the right and consequently the linear regression more horizontal. If gene frequency reached a point where only groups of type 4 and 5 are represented, the between-group regression might be actually horizontal. Looking at the regressions within groups, these show a fairly uniform disadvantage to altruists relative to non-altruists.

Thus, it is clear that eventually within-group and between-group components of selection will balance and a permanent polymorphism will result. In general, any convexity in a curved regression line of group fitnesses should suggest the possibility of a stable equilibrium. Note that "overdominance in fitness" for the group means does not have to hold for equilibrium to result.