Consider a population of creatures. Each creature has a "fitness". When two creatures of fitness x and y mate, they have $(x + y)/2$ offspring, each with fitness $(x + y)/2$.

In a "normal" population, all creatures have fitness 1. We assume that one of our many creatures (the "sport") deviates by having fitness 2. Call this generation zero.

Jenkin's Model. The sport, with fitness 2, mates with a creature of fitness 1, producing 1.5 offspring of fitness 1.5. The population is (implicitly) assumed to be large enough so that sports essentially never mate with other sports. Thus in generation one, each of the 1.5 sports mates with a creature of fitness 1, producing 1.25 descendants each of fitness 1.25; the total number of descendants is 1.25×1.5. In generation k, the sport has

$$g_k = \prod_{i=1}^{k} \left(1 + \frac{1}{2^i}\right)$$

descendants, each of fitness

$$f_k = 1 + \frac{1}{2^k}$$

.

The total number of descendants can never exceed

$$\prod_{i=1}^{\infty} \left(1 + \frac{1}{2^i}\right) \approx 2.38$$

Define the "sport value" of a generation to be (Total Fitness) minus (Population Size). Then the sport value in generation k never exceeds $\frac{1}{2^k} \times 2.38$ and hence goes rapidly to zero:

Generation	**# Sports**	**Fitness per sport**	**Sport value**
0	1	2	1
1	1.5	1.5	.75
2	1.875	1.25	.46875
...			
∞	2.38	1	0

Davis's Model. In Jenkin's model, a typical creature mates once per generation and produces one offspring, so the population size goes quickly to zero. We can correct for this by letting each creature mate *twice* per generation. Thus our original sport has 3 offspring, each of fitness 1.5. These collectively have 7.5 offspring, each of fitness 1.25, etc.

In generation k, the number of sports is

$$g_k = 2^k \prod_{i=1}^{k} \left(1 + \frac{1}{2^i}\right)$$

each with fitness

$$f_k = 1 + \frac{1}{2^k}$$

The sport value is therefore

$$\frac{1}{2^k} g_k \to 2.38$$

Generation	**# Sports**	**Fitness per sport**	**Sport value**
0	1	2	1
1	3	1.5	1.5
2	7.5	1.25	.1.875
...			
∞	∞	1	2.38

Criticism. Jenkin's model fails by predicting a population size that shrinks rapidly to zero. Davis's model fails in the opposite direction by predicting a population size that grows without bound.

In Jenkin's case, no account is taken of the fact that as the population shrinks, sports will eventually have to start mating with each other.

In Davis's case, no account is taken of the fact that as the sport population grows, sports will eventually have to start mating with each other.

A Better Model. We fix the population size by assuming that every pair of creatures mates once per generation, and that the offspring are "culled" to restore the original population size. (The culling is proportional, so that if, for example, 3/8 of the offspring have fitness 1.25, then 3/8 of the culled have fitness 1.25.)

This not only avoids the twin problems of population converging to zero or diverging to infinity, it also allows us to account for inbreeding among the sports (unlike either Jenkin or Davis).

Suppose there are initially (in generation zero) n creatures, of whom $n-1$ have fitness 1 and one has fitness 2. There are $(n-1)(n-2)/2$ matings among the "normal" creatures, each producing an offspring of fitness 1. There are $n-1$ matings between the sport and a normal creature, each producing 1.5 offspring of fitness 1.5.

In any future generation, suppose there are A creatures of fitness a, B creatures of fitness b, etc. There are $A(A-1)/2$ a-to-a matings, each producing a offspring of fitness a. There are AB a-to-b matings, each producing $(a+b)/2$ offspring of fitness $(a+b)/2$, and so forth.

For the reader who wants to make sure he's got it we give a numerical example with $n = 10$. In generation 0, we have (by assumption)

# Creatures	**Fitness**
9	1
1	2

with an average fitness of 1.1 and hence an average sport value of .1.

In generation 1 (without culling), we have

# Creatures	**Fitness**
36	1
13.5	1.5

with an average fitness of 1.136364 and therefore an average sport value of .136364. These averages are unaffected by the culling, so we continue to compute as if we haven't culled.

In generation 2 (still not culling), we have

# Creatures	**Fitness**
630	1
607.5	1.25
126.5625	1.5

for an average sport value of .157732.

And so forth.

Now continue to start in generation 0 with $n-1$ normal creatures and a single sport with fitness 2. Let a_k be the average sport value in generation k, so that $a_0 = 1/n$.

It is not hard to prove that $a_k = q_k(n)a_{k-1}$ where q_k is a rational function, increasing in the region where $n \geq 2$ and converging at infinity to $1 + \frac{1}{2^k}$

Therefore for all k, we have

$$a_k/a_0 < \prod_{i=k}^{\infty}\left(1 + \frac{1}{2^i}\right) = 2.38$$

In other words, the average sport value after any number of generations is bounded above by $2.38/n$.

With small populations, the bound is lower. For example, when $n = 2$, we have two creatures, of fitness 1 and 2, for an average sport value of .5. They mate once and have 1.5 offspring of fitness 1.5; thereafter the entire population has fitness 1.5 for an average sport value of .5, which is less than the allowable 2.38/2.

On the other hand, with a population of 1000, so that the average sport value in generation 0 is 1/1000, the average sport value by generation 6 has already reached .00234, which is pretty close to the bound of .00238. So for any reasonably sized population, the sport value does get close to 2.38/n pretty quickly.

Comparison

Starting with a population size of n containing a single sport, (and hence a total sport value of 1 and average sport value of $1/n$) we have the following predictions after a large number of generations:[1]

	Population	**TotalSportValue**	**AverageSportValue**
Jenkin	0	0	0
Davis	∞	2.38	0
Ours	n	2.38	$2.38/n$

Is this good or bad for Darwin? We find that an initial sport value is magnified over time by the factor 2.38, which is better than zero but not as good as, say a factor of the form Ck where k is the number of generations. Our model confirms both that a single mutation can have a lasting effect and that the lasting effect is small.

[1] In an earlier version of this table, I had the average sport value equal to 2.38 for the Jenkin model; Snorri Godhi caught and corrected the error.