Sex Ratios and the Power of Game Theory

The sex ratio is the ratio of males to females in a population

Sex Ratios Are Approximately 50:50 In Most Species

from eggs or caterpillars, I have received only the few following cases:—

	Males.	Females.
The Rev. J. Hellins[65] of Exeter reared, during 1868, imagos of 73 species, which consisted of	153	137
Mr. Albert Jones of Eltham reared, during 1868, imagos of 9 species, which consisted of	159	126
During 1869 he reared imagos from 4 species, consisting of	114	112
Mr. Buckler of Emsworth, Hants, during 1869, reared imagos from 74 species, consisting of	180	169
Dr. Wallace of Colchester reared from one brood of Bombyx cynthia	52	48
Dr. Wallace raised, from cocoons of Bombyx Pernyi sent from China, during 1869	224	123
Dr. Wallace raised, during 1868 and 1869, from two lots of cocoons of Bombyx yama-mai	52	46
Total	934	761

Including Humans

Image courtesy of hoyasmeg on Flickr. CC-BY

Puzzle:

Why are sex ratios at birth approximately 50:50 in most species?

Is it to ensure that everyone has a mate?

being more females than males. Put another way, males apparently have a tendency to suffer higher mortality rates than females. This is true for those dragonflies for which there are data (Corbet, Longfield, & Moore 1960), for the house fly (Rockstein 1959), for most fish (Beverton & Holt 1959), for several lizards (Tinkle 1967, Harris 1964, Hirth 1963, Blair 1960, Trivers, discussed below) and for many mammals (Bouliere & Verschuren 1960, Cowan 1950, Eisenberg 1965, Robinette et al. 1957, Beer, Frenzel, & MacLeod 1958, Stephens 1952, Tyndale-Biscoe & Smith, 1969, Myers & Krebs, 1971, Wood 1970). Hamilton (1948) and Lack (1954) have reviewed studies on other animals suggesting a similar trend. Mayr

From: Trivers 1976

Is it to maximize the size of the species?

No.

The real answer, thanks to Fisher (1930)

Simplest case:

- Female and male babies require approximately the same parental investment
- No inbreeding
- All males are expected to have the same number of offspring (same for females)

FACT:

Every child must have exactly one mother and one father

Suppose there are:

100 offspring
100 parents: 75 females, and 25 males

Each male expects 100/25 = 4 offspring
Each female expects 100/75 = 1.33 offspring

Males have more offspring

Parents of males have more grandkids

If everyone else gives birth to offspring at a ratio of 1 male to every 3 females (25:75)

You'd do better by having more male offspring

25:75 is not a Nash Equilibrium

Same argument holds for any sex ratio

Except 50:50

Then, male and female offspring have the same expected number of offspring

And you can’t do better by having more male or female offspring

50:50 is the unique Nash Equilibrium

Are we sure evolution will lead to 50:50?

If everyone gives birth to offspring at a ratio of 3 females for every male (25:75)

A mutant gene arises that leads to more male offspring

The individual with the mutant gene will have more grandkids, and the gene will end up disproportionally represented in two generations

Since individuals with this gene have more male offspring, this would increase the sex ratio

Until… the population hits 50:50

At 50:50, the mutant's male offspring won't give more grandkids

And the mutant will stop spreading

At 50:50, no mutant does better than existing population

And if it does by chance, the mutant will do worse and we'll return to 50:50

Evolution leads to Nash Equilibrium

Robust

Doesn’t matter if:

Males die before maturity, since result is driven by the expected number of children

Polygyny, for same reason

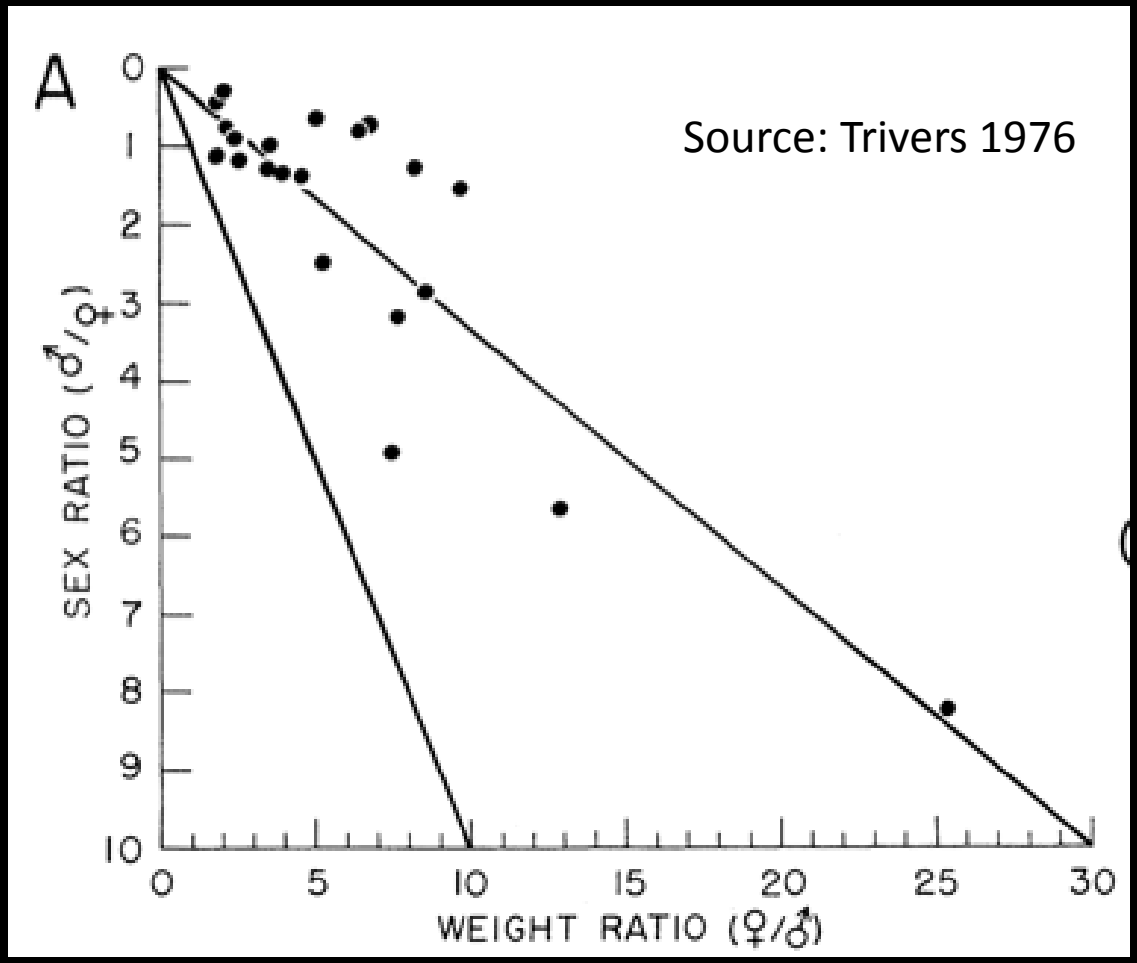
Population size isn’t constant

Sex determined by one sex

Wait a minute.

Sex ratios aren't *always* 50:50!

Sex Ratios vs. Parental Investment



Sex Ratios Amongst Inbred Wasps

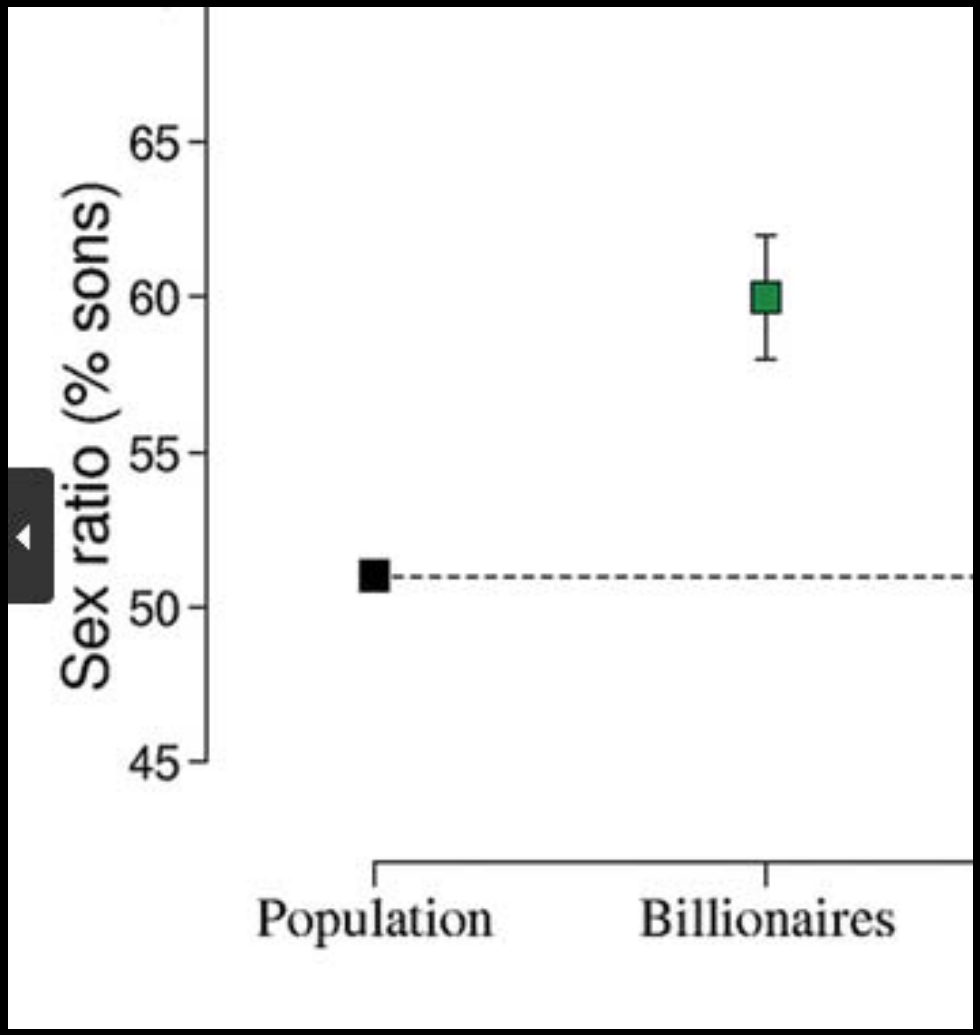
Table 1 Characteristics of fig wasp broods sampled in the wild

Fig (*Ficus*) species	No. of fruit crops sampled	Proportion of fruits with single-foundress broods	*n*†	Arithmetic mean of no. of foundresses	Single-foundress broods		Two-foundress broods	
					Mean proportion of males	No. of broods sampled	Mean proportion of males	No. of broods sampled
F. paraensis	15	0.97	1.01	1.03	0.056	28	0.079	25
F. pertusa	8	0.95	1.03	1.05	0.105	59	0.143*	10
F. bullenei	6	0.86	1.08	1.18	0.065	11	0.135*	7
F. obtusifolia	17	0.83	1.10	1.21	0.052	45	0.118	17
F. citrifolia	21	0.80	1.11	1.24	0.056	29	0.146	50
F. maxima	10	0.70	1.32	1.48	0.106	17	0.170*	14
F. yoponensis	7	0.60	1.39	1.64	0.114	8	0.188*	8
F. nymphiifolia	12	0.57	1.44	2.32	0.054	27	0.195*	10
F. dugandii	7	0.54	1.75	2.35	0.106	8	0.187*	6
F. popenoei	16	0.36	1.82	2.33	0.099	8	0.200*	15
F. insipida	33	0.27	1.98	3.11	0.136	54	0.288	21
F. near *trigonata*	9	0.35	2.05	2.53	0.107	17	0.178	25
F. trigonata	10	0.07	3.46	4.68	0.203	14	0.250*	9

Each fruit crop represents 20 individual fruits sampled at random.
† Inverse of the estimated proportion of sib-mated females.
* Predicted optimal brood sex ratio is within the 95% confidence interval of the observed mean sex ratios.

Source: Herre 1987

Sex Ratios Amongst Billionaires' Kids



Cameron, Elissa Z., and Frederik Dalerum. "A Trivers-Willard Effect in Contemporary Humans: Male-Biased Sex Ratios among Billionaires." *PLoS ONE* 4, no. 1 (2009): e4195. CC BY.

These exceptions are actually predicted by the theory

What if parents invest more in one sex?

Suppose females twice as costly to make as males

Is 50:50 an equilibrium?

Male and female offspring yield the same number of grandkids

But male offspring cost ½ as much

If everyone else gives birth to offspring at a ratio of one male to every female (50:50)

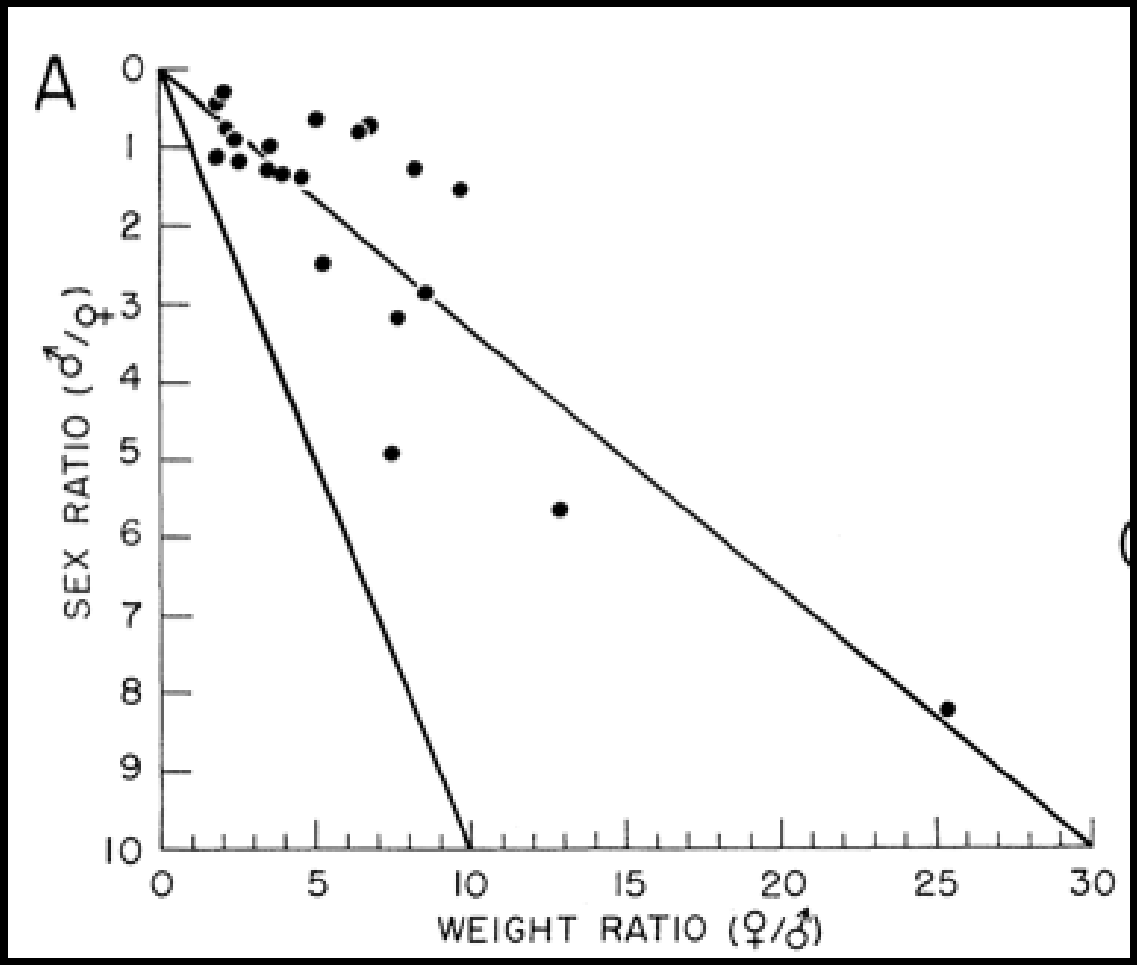
You wouldn’t choose this ratio

You would choose to take each female offspring and convert it to two male offspring

50:50 is not a Nash Equilibrium

In equilibrium, would have more males

Novel prediction that fits the data!



What if there is inbreeding?

Male offspring mate only with their sisters

Maximize number of grandkids by having mostly females

Novel prediction that fits the data!

Table 1 Characteristics of fig wasp broods sampled in the wild

Fig (*Ficus*) species	No. of fruit crops sampled	Proportion of fruits with single-foundress broods	*n*†	Arithmetic mean of no. of foundresses	Single-foundress broods		Two-foundress broods	
					Mean proportion of males	No. of broods sampled	Mean proportion of males	No. of broods sampled
F. paraensis	15	0.97	1.01	1.03	0.056	28	0.079	25
F. pertusa	8	0.95	1.03	1.05	0.105	59	0.143*	10
F. bullenei	6	0.86	1.08	1.18	0.065	11	0.135*	7
F. obtusifolia	17	0.83	1.10	1.21	0.052	45	0.118	17
F. citrifolia	21	0.80	1.11	1.24	0.056	29	0.146	50
F. maxima	10	0.70	1.32	1.48	0.106	17	0.170*	14
F. yoponensis	7	0.60	1.39	1.64	0.114	8	0.188*	8
F. nymphiifolia	12	0.57	1.44	2.32	0.054	27	0.195*	10
F. dugandii	7	0.54	1.75	2.35	0.106	8	0.187*	6
F. popenoei	16	0.36	1.82	2.33	0.099	8	0.200*	15
F. insipida	33	0.27	1.98	3.11	0.136	54	0.288	21
F. near *trigonata*	9	0.35	2.05	2.53	0.107	17	0.178	25
F. trigonata	10	0.07	3.46	4.68	0.203	14	0.250*	9

Each fruit crop represents 20 individual fruits sampled at random.
† Inverse of the estimated proportion of sib-mated females.
* Predicted optimal brood sex ratio is within the 95% confidence interval of the observed mean sex ratios.

What if all males don’t have approximately the same number of offspring (or females)?

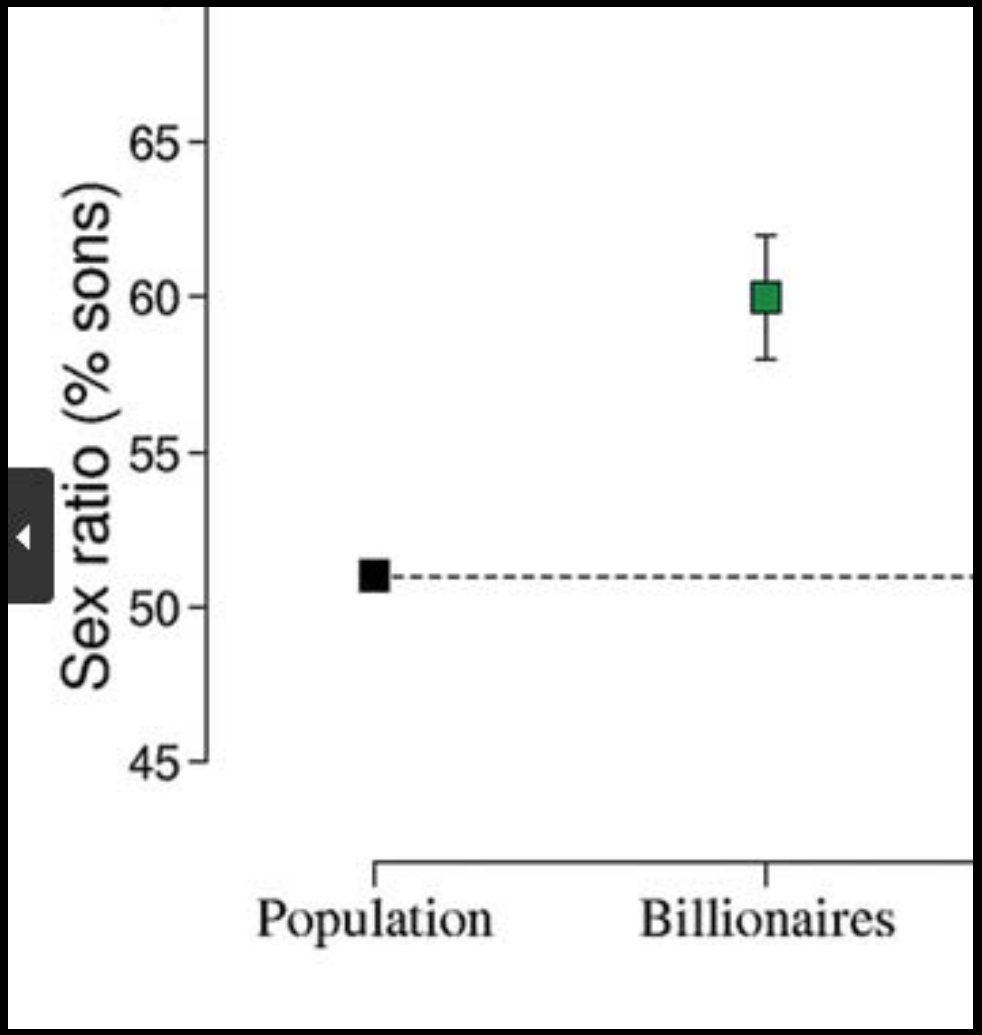
FACT: Males have a higher maximal number of offspring

Males benefit more from abundance of resources.

Males benefit more from having successful parents

Successful parents benefit more from having males

Novel prediction that fits the data!



Cameron, Elissa Z., and Frederik Dalerum. "A Trivers-Willard Effect in Contemporary Humans: Male-Biased Sex Ratios among Billionaires." *PLoS ONE* 4, no. 1 (2009): e4195. CC BY.

Our analysis of sex ratios is the gold standard for treating game theory as a science

Identify A Puzzle:

Why are sex ratios at birth approximately 50:50 in most species?

from eggs or caterpillars, I have received only the few following cases:—

	Males.	Females.
The Rev. J. Hellins[65] of Exeter reared, during 1868, imagos of 73 species, which consisted of	153	137
Mr. Albert Jones of Eltham reared, during 1868, imagos of 9 species, which consisted of	159	126
During 1869 he reared imagos from 4 species, consisting of	114	112
Mr. Buckler of Emsworth, Hants, during 1869, reared imagos from 74 species, consisting of	180	169
Dr. Wallace of Colchester reared from one brood of Bombyx cynthia	52	48
Dr. Wallace raised, from cocoons of Bombyx Pernyi sent from China, during 1869	224	123
Dr. Wallace raised, during 1868 and 1869, from two lots of cocoons of Bombyx yama-mai	52	46
Total	934	761

Use Data to Eliminate Alternative Explanations

- Ensure equal ratio at maturity?
- Maximize size of species?

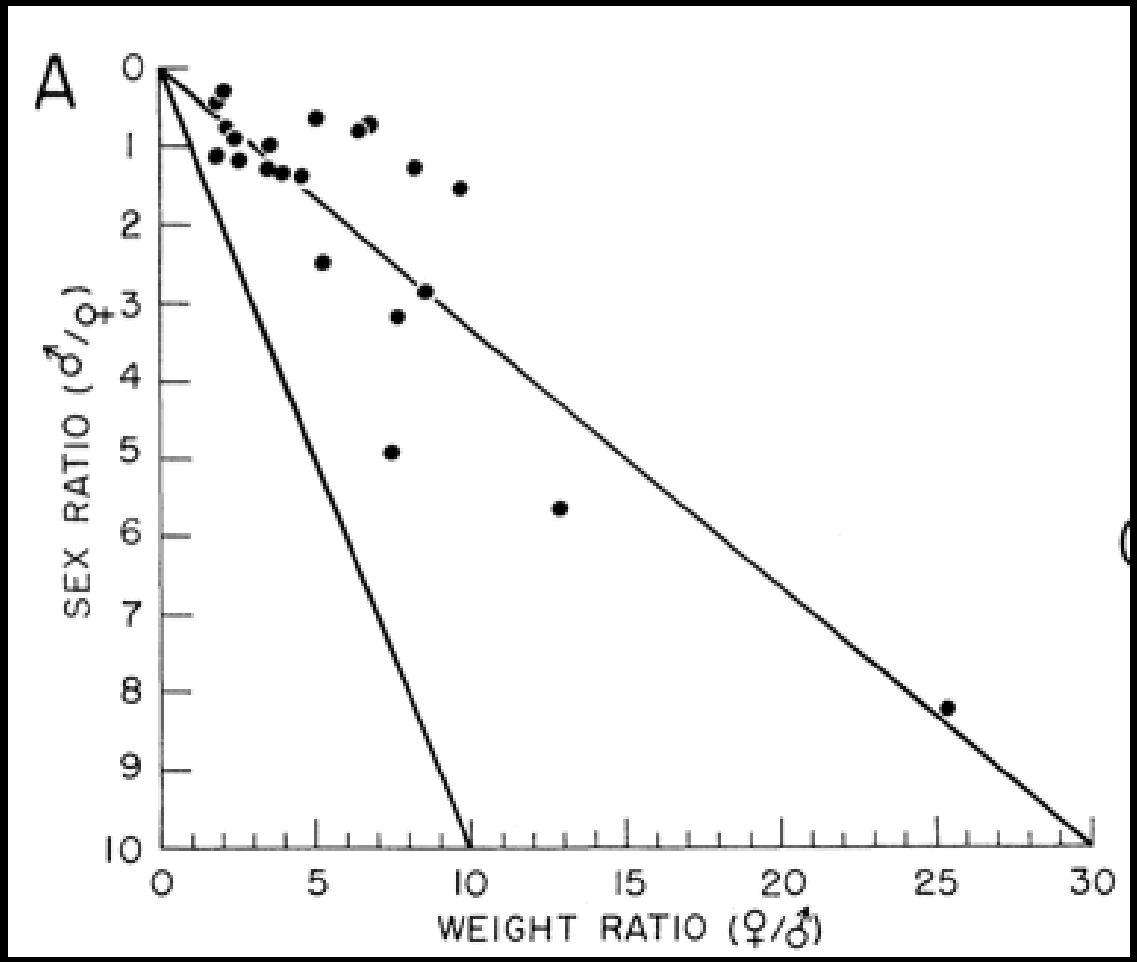
Use Game Theory to solve the puzzle

(in a way that's robust)

Use the theory to find novel predictions

If females require more parental investment, there will be more males in equilibrium

Find Empirical Evidence to Support It



14.11 Insights from Game Theory into Social Behavior
Fall 2013