40 (1622)

Differential survival of male and female dove embryos in increased and decreased pressures of oxygen: A test of the metabolic theory of sex.

By OSCAR RIDDLE.

[*From the Carnegie Station for Experimental Evolution, Cold Spring Harbor, N. Y.*]

Several kinds of evidence have been accumulated which indicate a metabolic difference between the ova (egg-yolks) which give rise to the two sexes in doves. A corresponding difference was also found in more limited investigations of adults of the two sexes. Our previous work has rather consistently indicated that female-producing eggs and female adults have a lower metabolism, males a higher metabolism. Since no metabolic studies upon male and female embryos have hitherto been made this study was carried out as a further necessary test of the complete applicability of the metabolic theory of sex to pigeons.

A method or means of measuring the metabolic differences between embryos of the two sexes is an enormously difficult thing to devise; and probably no plan is devisable at present which does not involve very much work. The many sources of error and difficulty in any attempt to measure heat-production, O_2-consumption of CO_2-production became embarrassingly evident when the unmeasurable and continually changing mass of the embryonic tissue is considered. The plan adopted by us was to subject—during one complete year—all or practically all of the embryos produced by the ring-doves and common pigeons of our collection to reduced and increased concentrations of oxygen (or to expose them to protracted periods of cold) and make such measurements and records as would probably reveal any relation of sex to survival under these conditions. Theoretically, if female embryos have a lower metabolism, *i.e.*, lower minimum oxygen requirement than males, the female embryos should withstand diminished pressures of oxygen somewhat better than male embryos. Similarly—since we had earlier learned that high pressures

of oxygen result in the death of some embryos—the male embryos should be somewhat better able than female embryos to withstand an increased concentration of oxygen. Again, if males have a higher metabolism than females the reduced metabolism induced by cooling should perhaps prove more harmful to the male embryos.

Embryos aged 3 minutes to 12 days have been used; but most frequently the age was between 1 hour and 4 days. Increased concentrations of oxygen varying from 26.8 per cent. to 96.6 per cent., and decreased concentrations varying from 18.3 per cent. to 0.15 per cent., were used. The time during which embryos were subjected to the altered pressures of oxygen varied from one to five days. For 0.15 per cent. O_2 the time was 15 minutes to 8 hours. Embryos were normally incubated under birds except during the period of treatment when moisture and temperature (39.4°) conditions were carefully controlled in the experimental chamber. In survival tests under "cooling" the eggs were either left at cold room temperature (50°–65° Fahr.) from 10–13 hours daily during several days or were placed at ice-box temperatures (8°–15° C.) during 18–24 hours. Sixty-five groups were tested in oxygen, 12 in cooling.

The age of the embryo has been found the most important factor in survival under alteration of the gaseous environment. Older embryos are most affected by reduced pressures of oxygen; younger embryos by increased pressures of oxygen. It is probable that the adequacy or thickness of the shell is also a factor in such survival. This adequacy of the shell has been painstakingly measured in all of the treated embryos.

The sex data from the reduced oxygen series have one notable defect. Eight embryos in which color was sex-linked were killed at an age when they should have shown eye-pigment or the lack of it which would declare their sex. Unfortunately, greatly reduced pressures of oxygen have been shown[1] wholly to prevent the post-mortem formation of this pigment and we have evidence that it at least interferes with its formation in these embryos. These eight embryos therefore could not be definitely classified and are omitted from the table. Embryos of known sex were not killed in about one half of the experiments. The lower half

[1] Riddle and La Mer, *Amer. Jour. Physiol.*, 1918, xlvii, p. 103.

SUMMARY OF SEX DATA FROM OXYGEN AND COOLING EXPERIMENTS.

Complete Data

Nature of Treatment.		No. of Embryos.	Embryos.				Sexes.								Surv'd. Sex Unknown.
			Killed.	Died very Soon.	Survived.	No Test.	Killed.		Survived.		Hatched.		Total.		
							♂	♀	♂	♀	♂	♀	♂	♀	
Incr. O_2.....	Totals.....	868	136	213	516	3	16	13	271	209	254	198	287	222	36
	Per cent....	—	15.7	24.5	59.3	0.3	5.6	5.9	94.4	94.1	**88.5**	**88.8**	129.6	100	7.0
Decr. O_2.....	Totals.....	792	284	64	434	10	34	22	190	204	176	190	224	226	40
	Per cent....	—	35.9	8.1	54.8	1.3	15.2	9.7	84.8	90.3	78.6	84.1	99.1	100	9.2
Cooling.....	Totals.....	440	212	—	226	2	34	21	106	113	—	—	140	134	7
	Per cent....	—	48.2	—	51.4	0.4	24.3	15.7	75.7	84.3	—	—	104.5	100	3.1
Only Experiments Showing "Sexed" Individuals Killed.															
Incr. O_2.....	Totals.....	450	86	152	210	2	16	13	107	79	98	74	123	92	20
	Per cent....	—	19.1	33.8	46.7	0.4	13.0	14.1	87.0	85.9	**79.7**	**80.4**	133.7	100	9.5
Decr. O_2.....	Totals.....	448	193	32	215	8	34	22	83	109	74	101	117	131	3
	Per cent....	—	43.1	7.1	48.0	1.8	29.1	16.8	70.9	83.2	63.2	77.1	89.3	100	10.7
Cooling.....	Totals.....	334	187	—	146	1	34	20	69	73	—	—	103	93	4
	Per cent....	—	56.0	—	43.7	0.3	33.0	21.5	67.0	79.5	—	—	110.8	100	2.7

of the table has therefore been constructed to eliminate those unrepresented experiments.

The table supplies a summary of the chief data obtained concerning sex. It will be understood that the sex of many embryos which were killed, and even of some which survived treatment but died too soon thereafter, could not be ascertained. It is clear that embryos which survive treatment with increased oxygen are about equally capable of completing the remainder of their embryonic development (hatching) regardless of sex. Perhaps the ability to "hatch," after proved survival, should not be considered as within the range of effects of treatment; but these data are given. The quite different sex ratios obtained from the increased oxygen experiments (129.6 ♂♂: 100♀♀) and from the decreased (99.1♂♂ : 100♀♀) is perhaps good evidence that the large number of killed and "unsexed" embryos of the first group contained disproportionate numbers of females, while the killed embryos of the second group probably included more males. The sex ratio from embryos subjected to cooling is of such quantity as to leave it a matter of doubt as to whether the killed and "unsexed" embryos differed in sex ratio from the survivors. This ratio nevertheless markedly differs from that obtained from increased oxygen. The known sex of the killed and of the survivors of this group also indicate clearly that the advantage here rests with the females.

The results are not wholly decisive but give some evidence that sex is also a factor in survival; further, that it is the males which best survive increased pressures of oxygen and females which best survive decreased pressures and cooling. Nearly all of the possible comparisons give the above result. The few figures which are opposed or seem questionable are placed in italics in the table.