

SIZE-FECUNDITY RELATIONSHIPS AND THEIR EVOLUTIONARY IMPLICATIONS IN FIVE DESMOGNATHINE SALAMANDERS

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The plethodontid salamander genus *Desmognathus* comprises seven species according to current taxonomy, of which six occur in, and four are endemic to the Appalachian Mountain system of eastern North America. Over most of the southern Blue Ridge Physiographic Province several of these forms may exist sympatrically. An apparent maximum of sympatry occurs in the Balsam Mountains of southwestern Virginia, where five species, *D. quadramaculatus*, *D. monticola*, *D. fuscus*, *D. ochrophaeus*, and *D. wrighti* occur in abundance.

Organ (1961) studied the ecological relationships and population dynamics of these species at Whitetop Mountain and Mt. Rogers in the Balsam Mountains. Hairston (1949) compared the ecologies of *D. quadramaculatus*, *D. monticola*, *D. ochrophaeus*, and *D. wrighti* in the Black Mountains of North Carolina where those four forms occur sympatrically. Both authors found that, in the order given above, these species form a series in which decreasing size is paralleled by an increasing tendency toward terrestrial habits. Organ further found that the trend is also paralleled by increasing juvenile survivorship. He concluded that heavier juvenile mortality is associated with aquatic sites, and that *D. quadramaculatus*, *D. monticola*, *D. fuscus*, *D. ochrophaeus*, and *D. wrighti* represent an evolutionary trend in which selection has favored progressively more terrestrial habits.

Size and egg production are positively correlated in the genus *Desmognathus*, as they are in many animals. Organ (1961) also emphasized that the larger species lay larger clutches than the smaller ones, and that the evolutionary trend within the

genus has been "the gradual transformation of a population with a high egg production and low survival into a population with low egg production and a high survival to maturity." He found no differences in number of clutches per year or age at maturity that might compensate for differences in clutch size.

This paper attempts to further explore and compare the relationships between size and fecundity among the five sympatric species of *Desmognathus* and to elaborate on the hypotheses drawn by Organ relative to evolutionary trends in reproductive habits. In particular I have sought to determine whether fecundity differences among the five species are explained simply by differences in their sizes, or whether size-fecundity relationships are more complex.

MATERIALS AND METHODS

This study is based mainly on Organ's series of *Desmognathus* from the Balsam Mountains. With regard to the species *wrighti* and *quadramaculatus*, I restricted this study to these series. I have included specimens of *D. monticola* from western North Carolina in addition to specimens from the Balsam Mountains in an attempt to include more of the total snout-vent length range for that species. Data on series of *D. ochrophaeus* from the vicinity of Highlands, North Carolina and *D. fuscus* from Licking County, Ohio are included where comparisons with Balsam Mountain material of those two species are appropriate.

Whenever possible, only females with eggs greater than 1 mm in diameter were examined. Otherwise it was difficult to distinguish smaller eggs from those to be deposited the following year, since in the

early stages of yolk deposition egg sizes are so variable as to obscure the differences between the clutches of successive years.

Snout-vent length measures the distance from the tip of the snout to the posterior angle of the vent. The method of covariance analysis was utilized to compare the slopes and elevations of the regression lines for the five species, using the methods and forms of calculations given in Snedecor (1956). The squared deviations and cross products of deviations were calculated from computer calculated raw sums, sums of squares, and sums of cross products. In the case of *D. quadramaculatus* rounding error prevented the use of computer calculated raw sums, and hand-calculated sums were used instead.

SUMMARY OF HABITS AND LIFE HISTORIES

The following accounts are based primarily on the studies of Hairston and Organ, supplemented in certain cases by my own observations.

Female Reproductive Cycles

Organ concluded that all five of the species deposit eggs biennially, but Martof and Rose (1963) found evidence for annual egg laying in *D. ochrophaeus* in the southern Appalachians. Tilley and Tinkle (1968) have presented evidence for an annual or possibly even biannual cycle in *D. ochrophaeus* in the vicinity of Mt. Mitchell and in the Balsam Mountains. Spight (1967) concluded that *D. fuscus* deposits eggs annually in eastern North Carolina and Harrison (1967) found that a sixth species, *D. aeneus*, also lays annually. Martof (1962) found evidence for biennial reproduction in another desmognathine, *Leurognathus marmoratus*.

The same weaknesses which Tilley and Tinkle found in the arguments for biennial egg laying in *D. ochrophaeus* probably apply as well to *D. wrighti*, *D. fuscus*, *D. monticola*, and *D. quadramaculatus*. Spight's study bears this out for *D. fuscus*.

Harrison's work indicates that annual egg laying may occur in *D. aeneus*. The evidence for bienniality in *Leurognathus* is not, in my opinion, compelling. In view of these arguments it would seem dangerous to assume bienniality in *D. wrighti*, *D. monticola*, and *D. quadramaculatus*. While more data on this point are sorely needed, I shall assume all five species dealt with here to be annual reproducers.

Nesting Habits

All five species exhibit parental care, in which the females remain with the eggs until hatching. Pope (1924) found that females of *D. monticola* and *D. quadramaculatus* attach each egg individually to the roof of the nesting cavity so that the eggs form a flat mass one or two eggs thick, whereas *D. fuscus*, *D. ochrophaeus*, and *D. wrighti* (information on the latter species from Organ, 1961) generally deposit their eggs in spherical clusters with only a few actually attached to the roof of the nesting cavity.

Females of the five species utilize somewhat different sites for egg deposition. *D. quadramaculatus* utilizes the most aquatic sites, depositing eggs on the undersides of rocks in the beds of streams and beneath small waterfalls. *D. monticola*, *D. ochrophaeus*, and *D. wrighti* deposit eggs in less aquatic sites than *D. quadramaculatus*, beneath stream banks and, in the case of *D. ochrophaeus*, beneath moss on rocks and logs in seepage areas. *D. fuscus* appears to lay eggs in situations intermediate between those utilized by *D. quadramaculatus* and those used by the other species.

Length of the Larval Period

The length of the larval period varies greatly among the five species, and reflects the aquatic to terrestrial trend discussed above. In the terrestrial *D. wrighti* metamorphosis occurs prior to hatching (one wonders, therefore, why it deposits its eggs in aquatic sites). Organ gave estimates of 26-28 months for *D. quadramaculatus*, 12-

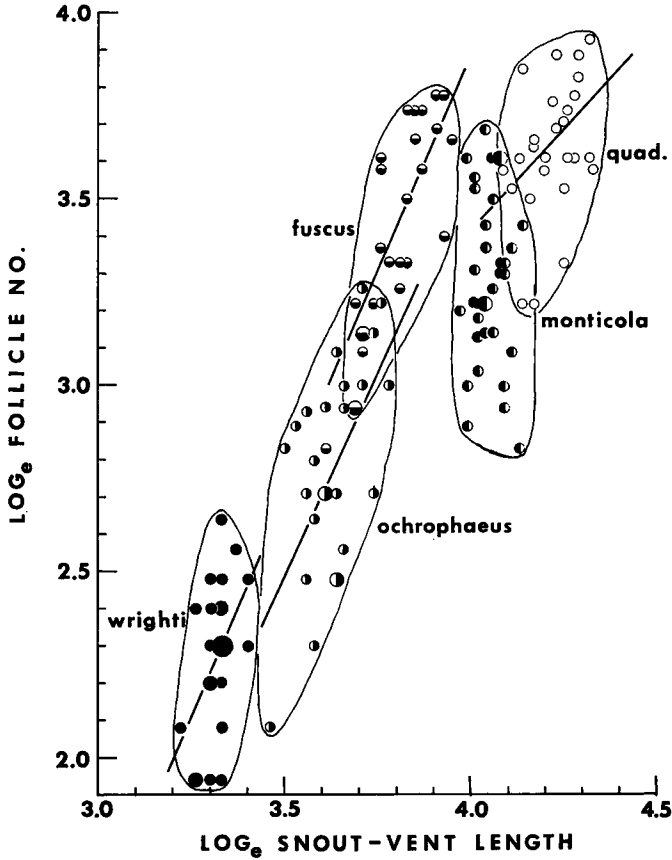


FIG. 1. Relationships between size and fecundity in five species of *Desmognathus*. Lines represent least squares regression lines of \log_{10} follicle number on \log_{10} snout-vent length.

13 months for *D. monticola*, 13–16 months for *D. fuscus*, and 10–11 months for *D. ochrophaeus*. The estimate for *D. ochrophaeus* is in error (Tilley and Tinkle, 1968); the larval period of that species is from 4 to 6 months at Mt. Mitchell, North Carolina.

Age at Maturity

Organ estimated that males of all five species matured at 3.5 years of age, while Spight (1967) estimated 3 years for males of *D. fuscus*. Both authors concluded that females require an additional year to produce their first clutch of eggs.

Habitats

D. quadramaculatus occurs chiefly in larger and faster streams, while *D. monti-*

cola prefers the banks of streams, as does *D. fuscus*. Organ found that both *D. ochrophaeus* and *D. wrighti* occur in terrestrial situations. Males of both species are largely terrestrial during the summer months, moving to aquatic sites such as seepage areas and spring heads during the winter. His data, as well as Hairston's and my own observations, indicate that of the two, *D. wrighti* is the more terrestrial. The aquatic sites preferred by *D. ochrophaeus* are of the seepage area-spring head variety, rather than the stream or stream side habitats occupied by *D. quadramaculatus* and *D. monticola*.

The species are also segregated altitudinally to a certain degree. *D. ochrophaeus* occurs from the lowest to the highest avail-

TABLE 1. Summary of regression data. n = sample size, r = correlation coefficient. Equations and correlation coefficients are for regressions of \log_e follicle number on \log_e snout-vent length. v = Balsam Mountains (Virginia), o = Ohio.

Species	n	r	Significance level	Regression equation
<i>D. wrighti</i>	23	0.458	0.050	$Y = 2.4130X - 5.7235$
<i>D. ochrophaeus</i>	25	0.598	0.010	$Y = 2.1773X - 5.1407$
<i>D. fuscus</i> (v)	26	0.837	0.001	$Y = 2.2845X - 5.2727$
<i>D. fuscus</i> (o)	18	0.687	0.010	$Y = 1.7484X - 3.3944$
<i>D. monticola</i>	35	-0.163	< 0.100	-
<i>D. quadramac.</i>	26	0.390	0.050	$Y = 1.0700X - 0.8825$

able habitats in the Appalachians. In the Balsam Mountains *D. fuscus* has a similar distribution, but does not extend as high as does *D. ochrophaeus*, while *D. quadramaculatus* and *D. monticola* occur from the lowest elevations in the Balsam Mountains to just above 5000 feet. Organ found that *D. fuscus* and *D. monticola* have mutually exclusive distributions, with *D. fuscus* occupying the banks of the headwaters of streams at high elevations and *D. monticola* occupying the banks of streams at lower elevations. *D. wrighti* is essentially a high elevation species, whose populations reach their maximum densities in the spruce-fir forests of the southern Appalachians. However, it extends to as low as 3000 feet near Mt. Mitchell (personal observation and Hairston, 1949) and Organ found it as low as 3500 feet in the Balsam Mountains.

RESULTS

Figure 1 shows the relationship between snout-vent length and follicle number in the five species studied. Plots of the untransformed data were curvilinear, presumably because follicle number is a function of body volume rather than body length. Furthermore, the variance in follicle number was positively correlated with snout-vent length. For these reasons both variables were converted to their natural logarithms, which are plotted in Figure 1. All of the statistics discussed below are based on the natural logarithms of the data.

The \log_e - \log_e transformation succeeded in making the variances along the regres-

sion lines relatively homogeneous, but not in removing all of the curvilinearity. *D. wrighti* appears to have somewhat higher \log_e follicle number values than might have been expected from extrapolation from the regression for *D. ochrophaeus*. *D. quadramaculatus*, on the other hand, appears to have slightly lower values. Table 1 gives the correlation coefficients and regression equations for the five species, Table 2 the results of the covariance analyses in which the regression for *D. ochrophaeus* was compared with those for the other four species. Whereas there is a suggestion of curvilinearity when all the species are graphed together, the regressions for *D. wrighti* and *D. quadramaculatus* do not differ significantly from that for *D. ochrophaeus* at the five percent level, neither with respect to the slopes nor to the elevations of the regression lines (Tables 2 and 3). The analysis suggests, rather, that the relationship between snout-vent length and fecundity is identical in the species *wrighti*, *ochrophaeus*, and *quadramaculatus*.

Since the correlation coefficient for *D. monticola* is insignificant (in fact, negative) at the five percent level, that species was excluded from the covariance analysis. The hypothesis that *D. monticola* lies on the regression line common to *D. wrighti*, *D. ochrophaeus*, and *D. quadramaculatus* was tested as follows: A single regression line was calculated for the three species, having the equation $Y = 1.5027X - 2.7020$. From this equation the mean \log_e follicle number corresponding to the mean \log_e snout-vent length was calculated (3.3931). This value

TABLE 2. Summary of covariance analyses. F tests for similarity of slopes and elevations constructed as in Snedecor, 1956. Subscripts as in Table 1. Based on log-log_e transform.

Test	Slopes		Elevations		Conclusions	
	F	Significance level	F	Significance level	Slopes	Elevations
Overall (less <i>monticola</i>)	1.100	< 0.05	27.235	0.01	equal	different
<i>ochrophaeus</i> vs. <i>wrightii</i>	0.040	< 0.05	1.754	< 0.05	equal	equal
<i>ochrophaeus</i> vs. <i>fuscus</i> (v)	0.024	< 0.05	10.273	0.01	equal	different
<i>ochrophaeus</i> vs. <i>fuscus</i> (o)	0.282	< 0.05	4.495	0.05	equal	different
<i>ochrophaeus</i> vs. <i>quadramac.</i>	1.821	< 0.05	0.349	< 0.05	equal	equal
<i>fuscus</i> (v) vs. <i>fuscus</i> (o)	0.786	< 0.05	5.373	0.05	equal	different

was compared with the actual value for *D. monticola* (3.3001) by means of a *t*-test. The resultant $t = 2.1577$, $df = 33$ is significant at the five percent level. Thus *D. monticola* appears to lay somewhat fewer than the expected number of eggs.

In order to further test the hypothesis that the relationship between clutch size and body size is the same in both *D. wrightii* and *D. ochrophaeus*, the clutch sizes of female *D. wrightii* were compared with those of very small female *D. ochrophaeus* from the southwestern portion of the latter's range near Highlands, North Carolina. These data were not analyzed statistically but, as shown in Figure 2, female *D. ochrophaeus* of the same size range as *D. wrightii* lay approximately the same number of eggs.

The overall covariance analysis (excluding *D. monticola*) shown in Tables 2 and 3 indicates that all five species lie on lines with the same slope, but that the hypothesis that all lie on a single line is rejected at the one percent level. Comparison of *D. ochrophaeus* with the other species has shown that it lies on the same regression line as *D. wrightii* and *D. quadramaculatus* but on a different line from *D. fuscus*. At any given size then, *D. fuscus* lays more eggs than *D. ochrophaeus* whereas the increase in fecundity per unit increase in size is the same for all the species. The mean number of eggs carried by females of *D. fuscus* examined (31.4), in fact, exceeded the mean number contained in females of *D. monticola* (28.1), although the difference

is not significant at the five percent level ($t = 1.0057$, $.4 > P > .3$). Thus *D. fuscus*, for its size, has a higher fecundity than any of the other species.

The Balsam Mountain region is one of the few areas in the Blue Ridge Physiographic Province where *D. fuscus* occurs, and is perhaps the only part of its extensive range where it is sympatric with as many other species of *Desmognathus*. It seemed possible, therefore, that the reproductive properties of the species in the Balsams might differ from those in other parts of its range. In order to test for such differences, the regression in the Balsam Mountain material was compared with that in a series of 19 females from Licking County, Ohio (UMMZ 125516-17). One of the latter was discarded from the analysis because she contained abnormally few follicles. The regressions are superimposed in Figure 3, and the results of the covariance analysis comparing them are given in Tables 2 and 3. The difference between the slopes is not significant at the five percent level but that between the elevations of the regression lines is, the elevation for the Balsam Mountain series being higher. Furthermore, the Balsam Mountain specimens are larger. Both of these factors would appear to indicate that *D. fuscus* in that region are considerably more fecund than at least those from the Ohio population.

The covariance analysis also indicates that Ohio specimens differ significantly from *D. ochrophaeus*, although less than Balsam Mountain *D. fuscus* do.

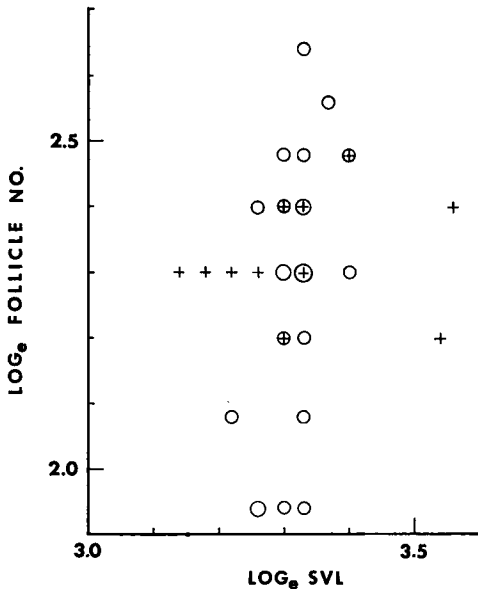


FIG. 2. Relationships between size and fecundity in *Desmognathus wrightii* (circles) from the Balsam Mountains and *D. ochrophaeus* (crosses) from Cullasaja Gorge near Highlands, North Carolina. Regression lines and transformations as in Fig. 1.

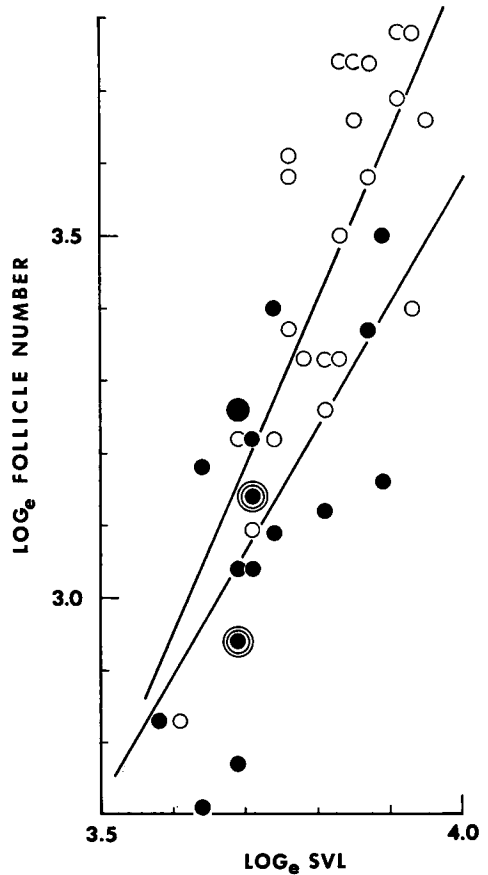


FIG. 3. Relationships between size and fecundity in *D. fuscus* from the Balsam Mountains (hollow circles) and Ohio (solid circles). Regression lines and transformations as in Fig. 1.

Assuming a constant egg volume-body volume relationship in the five species, the regression of clutch size on body length would appear to indicate that a reasonably constant relationship is maintained between clutch volume and body volume, at least among the species *wrightii*, *ochrophaeus*, and *quadramaculatus*. From the comparison of regressions one might expect that the ratio of clutch volume to body volume is higher in *D. fuscus* and lower in *D. monticola*. Ratios were calculated for the specimens examined, and their means among the five species are compared in Figure 4. The clutch volumes were based on the diameters of the largest eggs found in each of the species. These were: *D. wrightii*, 2.5 mm; *D. ochrophaeus*, 3.0 mm; *D. fuscus*, 3.0 mm; *D. monticola*, 4.0 mm; and *D. quadramaculatus*, 4.0 mm. Body volumes were calculated as perfect cylinders using snout-vent length as length and width at the axilla as diameter. The ratios of axillary width to snout-vent length were

compared among the five species. Those species between which the ratios did not differ significantly at the five percent level were all assigned the ratios' mean value for those species. Trunk-length to body-length ratios were also compared and found not to differ significantly at the five percent level among the five species. Thus snout-vent length could be used to compute body volumes. Body volumes were then calculated as the following functions of snout-vent lengths: *D. wrightii*, *D. ochrophaeus*, and *D. fuscus*, $V = .0142(SVL^3)$; *D. monticola*, $V = .0191(SVL^3)$; and *D. quadramaculatus*, $V = .0172(SVL^3)$.

TABLE 3. Details of individual covariance analyses, constructed after Snedecor, 1956. f = degrees of freedom; x = deviations from \log_e mean snout-vent lengths, y = deviations from \log_e mean follicle numbers, b = slopes, SS = sum of squared deviations from regression line, MS = mean squared deviations from regression line (residual variances).

Source	Deviations from means				Deviations from reg.			
	f	Σx^2	Σxy	Σy^2	b	j	SS	MS
<i>wrighti</i>	22	0.0414	0.0999	0.9482	2.4130	21	0.7071	0.0336
<i>ochrophaeus</i>	24	0.1618	0.3523	2.1465	2.1773	23	1.3795	0.0599
<i>fuscus</i>	25	0.2390	0.5460	2.0302	2.2845	24	0.7829	0.0326
<i>quadramac.</i>	25	0.1128	0.1207	0.8542	1.0700	24	0.7251	0.0302
Pooled						92	3.5946	0.0390
Reg. coef.						3	0.1288	0.0429
Common		0.5550	1.1189	5.9791	2.0160	95	3.7234	0.0391
Adj. means						3	3.1948	1.0649
Total		11.1105	17.3461	33.9995		98	6.9182	
<i>ochrophaeus</i>	24	0.1618	0.3523	2.1465	2.1773	23	1.3795	0.0599
<i>wrighti</i>	22	0.0414	0.0999	0.9482	2.4130	21	0.7071	0.0336
Pooled						44	2.0866	0.0474
Reg. coef.						1	0.0019	0.0019
Common		0.2032	0.4522	3.0947	2.2253	45	2.0885	0.0464
Adj. means						1	0.0814	0.0814
Total		1.3800	2.2639	5.8838		46	2.1699	
<i>ochrophaeus</i>	24	0.1618	0.3523	2.1465	2.1773	23	1.3795	0.0599
<i>fuscus</i> (v)	25	0.2390	0.5460	2.0302	2.2845	24	0.7829	0.0326
Pooled						47	2.1624	0.0460
Reg. coef.						1	0.0011	0.0011
Common		0.4008	0.8983	4.1767	2.2412	48	2.1635	0.0450
Adj. means						1	0.4623	0.4623
Total		0.7731	2.3092	9.5231		49	2.6258	
<i>ochrophaeus</i>	24	0.1618	0.3523	2.1465	2.1773	23	1.3795	0.0599
<i>quadramac.</i>	25	0.1128	0.1207	0.8542	1.0700	24	0.7251	0.0302
Pooled						47	2.1046	0.0447
Reg. coef.						1	0.0814	0.0814
Common		0.2746	0.4730	3.0007	1.7225	48	2.1860	0.0455
Adj. means						1	0.0159	0.0159
Total		4.7530	7.0763	12.7371		49	2.2019	
<i>fuscus</i> (v)	25	0.2390	0.5460	2.0302	2.2845	24	0.7829	0.0326
<i>fuscus</i> (o)	17	0.1276	0.2231	0.8261	1.7484	16	0.4360	0.0256
Pooled						40	1.2189	0.0304
Reg. coef.						1	0.0239	0.0239
Common		0.3666	0.7691	2.8563	2.0979	41	1.2428	0.0303
Adj. means						1	0.1628	0.1628
Total		0.4247	0.9956	3.7394		42	1.4056	
<i>ochrophaeus</i>	24	0.1618	0.3523	2.1465	2.1773	23	1.3795	0.0599
<i>fuscus</i> (o)	17	0.1276	0.2231	0.8261	1.7484	16	0.4360	0.0256
Pooled						39	1.8155	0.0465
Reg. coef.						1	0.0131	0.0131
Common		0.2894	0.5754	2.9726	1.9882	40	1.8286	0.0457
Adj. means						1	0.2162	0.2162
Total		0.3878	0.9404	4.3253		41	2.0448	

The ratios for the five species are graphed in Figure 4. Non-overlap of the black boxes, representing twice the standard error on either side of the means, indicates mean differences significant at approximately the five percent level. As expected from the covariance analysis, *D. fuscus* is characterized by the highest ratios of the five species, and differs significantly from all but *D. ochrophaeus*. The mean ratio for *D. ochrophaeus* is significantly higher than those for *D. wrightii* and *D. quadramaculatus*. No significant differences occur among the latter three species. Thus, while *D. wrightii*, *D. ochrophaeus*, and *D. quadramaculatus* lie on the same regression line when follicle number is plotted against snout-vent length, this regression does not maintain a constant clutch volume-body volume ratio among the three species using the criteria for calculating clutch and body volumes given above.

DISCUSSION

Fecundity is only one of many variables subject to adjustment by natural selection in the maximization of individual fitness. In the genus *Desmognathus* fecundity is intimately related to body size, both within and between species. At the interspecific level, however, this relationship is not perfect. Considering the variety of habitats exploited by the species dealt with here, perhaps it is closer than one would intuitively expect, particularly among the series *wrightii*, *ochrophaeus*, and *quadramaculatus*. Any theory concerned with the evolutionary modification of demographic parameters in the genus *Desmognathus* must somehow explain both the overall closeness of this relationship and its imperfections.

One means of reconciling the similarity of the relationship in these species with the diversity of their habitats would be to conclude that selection is able to increase fecundity only by increasing body size, and that high fecundities are selectively advantageous in aquatic habitats. This would ignore the imperfections of the relationship

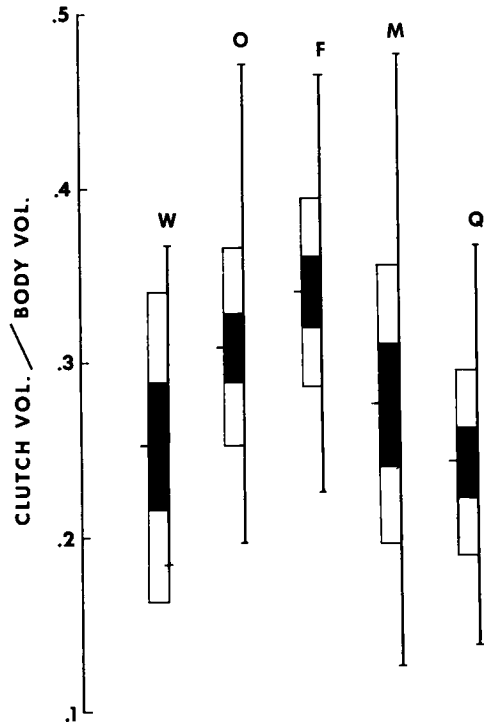


FIG. 4. Comparison of clutch volume-body volume ratios among the five species of *Desmognathus*. Solid boxes represent twice the standard error, hollow boxes one standard deviation on either side of each mean.

between size and fecundity and, more seriously, leaves unanswered the question of the selective advantage of high fecundity in aquatic habitats. Organ's (1961) data show mortality to be heavier in such situations, but to hypothesize that this results in selection for increased fecundity violates the arguments of Lack (1954), who pointed out that high mortality rates result from high fecundities.

Assuming, as most authors have, that aquatic situations are the ancestral habitat of the genus *Desmognathus* (Dunn, 1926; Wake, 1966), and that body size differences were established in advance of terrestrial tendencies in the smaller forms, selection operating whenever the various species came into contact might have re-

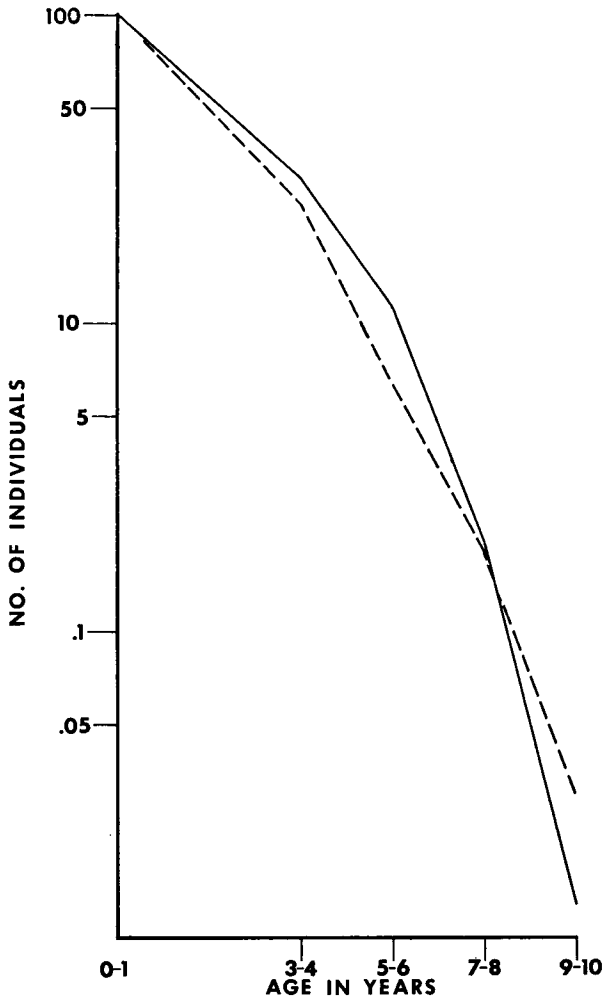


FIG. 5. Survivorship curves for males of *D. fuscus* (solid line) and *D. monticola* (broken line) from the Balsam Mountains. Data on numbers of individuals in successive year classes from Organ, 1961. See text for additional explanation.

sulted in their displacement into different habitats. Terrestrial tendencies would have been most strongly favored in the smaller forms, since these were (and still are) subject to predation by larger salamanders. The latter, by virtue of their size, would have been able to remain in the ancestral habitat.

The data presented in this paper indicate that positive size-fecundity correlations are evident both within and between

the species examined. It seems reasonable to assume that such correlations also held among the ancestors of the present forms, so that the larger forms were also the most fecund, just as they are today. This, in turn, would have led to the higher juvenile mortality rates among aquatic species that Organ observed in his data.

The data on clutch volume-body volume ratios suggest that egg size, as well as clutch size has been altered in the evolution

of the reproductive rates of the forms studied. Thus *D. ochrophaeus*, while it lies on the same size-fecundity regression line as *D. wrighti* and *D. quadramaculatus*, is characterized by a higher clutch volume-body volume ratio than either of those two species. *D. monticola*, on the other hand, lays fewer eggs than expected from the *wrighti-ochrophaeus-quadramaculatus* regression, but evidently amasses the same relative volume of yolk per clutch.

Clutch volume-body volume ratios are probably more meaningful indications of the actual amount of effort expended at each reproduction than are clutch sizes alone, and do not appear to correlate at all closely with the aquatic to terrestrial trend. *D. fuscus* is particularly discrepant in this regard (Fig. 4), as well as in its average clutch size (Fig. 1). Of the five species considered here, *D. fuscus* is the only one in which the adults have not evolved some means of minimizing predation by larger salamanders in aquatic habitats. *D. quadramaculatus* and *D. monticola* share the advantage of large size. Mature males of *D. ochrophaeus* and both sexes of *D. wrighti* are largely terrestrial during most of the year. The fact that brooding females of both *D. ochrophaeus* and *D. fuscus* are probably subjected to heavier mortality than the other species should cause selection to favor greater reproductive efforts per season (Williams, 1966). Figure 5 compares the survivorship curves for males of *D. fuscus* and *D. monticola*, based on Organ's data for numbers of males in different year classes and mine on fecundities (Organ assumed a larger clutch size in *D. monticola*, based on clutches of the two species that he found in the field). The curves, similar as they are, do indicate slightly lower adult survivorship in *D. fuscus*. Since in these two species both sexes occupy similar habitats, female survivorship curves of the two should exhibit a similar relationship to one another. Organ estimated the mean annual survival rate of brooding females of *D. fuscus* to be the lowest of the five species. However,

since he concluded that the species had a biennial laying cycle he also assumed that he could distinguish between females that had brooded during the previous year and those which would produce eggs during the current year, and used this information to calculate the mean annual survival rate for brooding females. Since Martof and Rose (1963) and Tilley and Tinkle (1968) have presented reasons for doubting the presence of a biennial laying cycle, the groups of animals that Organ compared probably did not represent groups of females that were depositing eggs in successive years. Thus, with our present inability to age female salamanders, it is extremely doubtful whether survivorship curves can be constructed for that sex.

If the shorter adult life expectancy of *D. fuscus* is in fact attributable to predation by large aquatic *Desmognathus*, one might expect the reproductive effort per season of individuals free of that source of mortality to be lower. Figure 3 indicates that this may in fact be the case. Female *D. fuscus* from the Balsam Mountains do lay more eggs than those from the Licking County, Ohio population. This is attributable both to their larger size and to a different size-fecundity relationship, whereby for any given size, females of the Balsam Mountain population lay more eggs than females from Ohio. Perhaps their larger size is also an adaptation directed toward increased fecundity.

The fact that *D. fuscus* combines relatively small size and aquatic habits may account for its absence throughout most of the southern Blue Ridge Physiographic Province, in which its preferred habitats are occupied by larger salamanders. As suggested by Dunn (1926) and Organ (1961), competition with *D. monticola*, as well as predation by it and other large salamanders, may be important in determining the distribution of *D. fuscus*.

SUMMARY

Size and fecundity are positively correlated in four of the five species of *Desmog-*

nathus inhabiting the Balsam Mountains of southwestern Virginia. This correlation is manifest both inter- and intraspecifically.

Size-fecundity relationships are identical in *D. wrighti*, *D. ochrophaeus*, and *D. quadramaculatus*, while *D. fuscus* has a higher and *D. monticola* a lower fecundity than expected by extrapolation of the common regression for the other three species. *D. fuscus* and *D. ochrophaeus* both exhibit higher clutch volume-body volume ratios than do the other species.

It is hypothesized that selection has favored terrestrial tendencies in the smaller species because of their vulnerability to predation by larger aquatic salamanders. The fact that the smaller species are necessarily less fecund has resulted in their exhibiting lower mortality rates. The relatively high reproductive efforts of *D. fuscus* and *D. ochrophaeus* may result from their combining relatively small size with aquatic habits.

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LITERATURE CITED

- HAIRSTON, N. G. 1949. The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. *Ecol. Monog.* 19:47-73.
- HARRISON, J. R. 1967. Observations on the life history, ecology and distribution of *Desmognathus aeneus aeneus* Brown and Bishop. *Amer. Mid. Natur.* 77(2):356-370.
- LACK, D. 1954. The evolution of reproductive rates. In J. S. Huxley, A. C. Hardy, E. B. Ford (eds.), *Evolution as a process*. Allen and Unwin, London.
- MARTOF, B. S. 1962. Some aspects of the life history and ecology of the salamander *Leurognathus*. *Amer. Mid. Natur.* 67(1):1-35.
- MARTOF, B. S., AND F. L. ROSE. 1963. Geographic variation in southern populations of *Desmognathus ochrophaeus*. *Amer. Mid. Natur.* 69(2):376-425.
- ORGAN, J. A. 1961. Studies of the local distribution, life history, and population dynamics of the salamander genus *Desmognathus* in Virginia. *Ecol. Monog.* 31:189-220.
- POPE, C. H. 1924. Notes on North Carolina salamanders, with especial reference to the egg-laying habits of *Leurognathus* and *Desmognathus*. *Amer. Mus. Nov.* 306:1-19.
- SNEDECOR, G. W. 1956. *Statistical methods*. Iowa State Univ. Press, Ames.
- SPIGHT, T. M. 1967. Population structure and biomass production by a stream salamander. *Amer. Mid. Natur.* 78(2):437-447.
- TILLEY, S. G., AND D. W. TINKLE. 1968. A re-interpretation of the reproductive cycle and demography of the salamander *Desmognathus ochrophaeus*. *Copeia* 1968(2):299-303.
- WAKE, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. *Mem. S. California Acad. Sci.* 4:1-111.
- WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Amer. Natur.* 100(916):687-690.