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ON THE VARIABILITY OF ALLIGATOR SEX RATIOS

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Serious investigations regarding natural selection for the sex ratio began with the hypothesis of Fisher (1958), who concluded that a population's sex ratio at the end of the period of "parental expenditure" should reflect equal expenditure on males and females. Thus, for species in which males and females incur the same costs to parents, a population sex ratio of .5 (where sex ratio is expressed as proportion males) at the end of this period should represent an evolutionary equilibrium. This argument assumes that genetic variability is associated with mechanisms of sex determination and that sex represents a heritable trait. Various quantitative models relating to Fisher's hypothesis have been developed and have generally supported the notion of natural selection favoring a .5 sex ratio in the absence of disparate costs incurred by the two sexes (Shaw and Mohler 1953; Shaw 1958; Bodmer and Edwards 1960; Kolman 1960; MacArthur 1965; Verner 1965; Leigh 1970; Crow and Kimura 1970; Hartl and Brown 1970; Charnov 1975; Leigh et al. 1976). This general hypothesis has also received empirical corroboration from the apparently widespread occurrence of sex ratios equal to .5 for well-studied animals. Nevertheless, examples of primary (at conception) and secondary (at the end of the period of parental care; definition follows Pianka 1974) sex ratios that differ significantly from .5 do exist. Such ratios seem to be more prevalent among invertebrates (see reviews in Hamilton 1967; Flanders 1946), but also appear to exist among some vertebrates (e.g. Crew 1937; Humphrey 1945; Weir 1960; Fitch 1961; Kosswig 1964; Verme 1969; Teitelbaum 1972; Mech 1975; Howe 1977; Pinkowski 1977; Shine and Bull 1977). Theoretical investigations and discussions of unequal sex ratios have emphasized inbreeding (Hamilton 1967; Hartl 1971), polygenic sex determination (Kosswig 1964), sex-specific differences in reproductive success associated with environments of varying quality (Trivers and Willard 1973; Charnov and Bull 1977; Charnov 1979), temporal changes in sex-specific life history expectations (Werren and Charnov 1978), and have also included suggestions regarding the possible importance of kin selection and group selection (Eshel 1975).

Some organisms exhibit considerable variability of the sex ratio. Such variation often seems to be related to environmental factors that exert effects by influencing

the physiological state of reproducing animals and/or by actually affecting sex determination in the offspring after conception (e.g., White 1954; Andersen 1961; Trivers and Willard 1973; Charnov and Bull 1977). Environmental influence on the sex ratio occurs in numerous invertebrates (Banta and Brown 1929a, 1929b; Christie 1929; Flanders 1939, 1942; Clausen 1939; Ellenby 1954; Battaglia 1963; Mackauer 1976). Sex ratio in some vertebrates also seems to be associated with environmental conditions (Verme 1969; Teitelbaum 1972; Mech 1975; Howe 1977; Trivers and Willard 1973; but see Myers 1978); and Wilson (1975, p. 317) has stated, "With physiological control of sex determination so prominently developed in the insects, the possibility should not be overlooked that it also occurs at least to a limited extent in the vertebrates." Here we examine empirical evidence on sex ratios in American alligators (*Alligator mississippiensis*). We use these data to test two hypotheses: (1) that the sex ratio of young alligators is .5 and (2) that sex ratios in young alligators from two different environments (wild populations and a "farm" population) are the same. The relevance of these results to theoretical predictions is discussed.

METHODS

Alligator sex ratios reported here are taken from wild populations in the coastal marshland of southwestern Louisiana and from a commercial alligator farm belonging to the Kliebert brothers near Hammond, Louisiana. Wild samples include original data from Chabreck as well as reports from the literature. The majority of Chabreck's sample was obtained on Rockefeller Wildlife Refuge. These alligators were located by travelling waterways by boat at night and shining their eyes with a headlight. All aquatic habitats with water areas large enough for air boat operation were examined. Small animals were captured by hand. Larger animals were captured by placing a wire noose mounted on a heavy pole around the neck. The noose was then tightened, and the alligator was pulled into the boat. Sex was determined by examining the cloaca for the presence or absence of a penis. Capturing and sexing techniques were described in detail by Chabreck (1963).

Farm samples reported here represent the progeny of wild-caught males and females that were caught as immatures and reared in captivity. The farm samples originated from the clutches of approximately 50–75 females that were inseminated in captivity. The young animals were kept in large concrete enclosures that were heated during winter months. Farm animals were fed generously and grew at faster rates than wild animals.

Alligators from both sets of samples were classified as adults and/or immatures. Alligators from wild Louisiana populations attain sexual maturity at a total body length of approximately 1.8 m (Giles and Childs 1949; Joanen and McNease 1973), and our age classification is based on this length. Immatures are especially relevant to our discussion and have thus been additionally classified into 0.3-m size intervals that can be tentatively related to age classes using growth rate data of Chabreck and Joanen (1979) and McIlhenny (1934) for wild Louisiana alligators. Farm alligators were reared in age-specific pens and all the animals reported here (with the possible exception of an occasional older animal which may have climbed into the pens) were 2 yr old.

Three statistical tests are used in this paper. Two of these tests are sometimes included under the general term "binomial test" (e.g., Siegel 1956) and are used to test the hypothesis that sample sex ratios are drawn from a population in which true sex ratio is .5. The first of these tests employs the cumulative distribution function of the binomial distribution and involves computation of the probability that x or fewer males (or females; whichever sex is fewer in number) would occur in a sample of size n if the probability of sampling a male (or female) is really .5 (i.e., $p = q = 0.5$). This probability of obtaining a value as extreme as x is computed as

$$P(x) = \sum_{i=0}^{x} \binom{n}{i} p^i q^{n-i},$$

and is used here for small sample sizes. For larger samples we use the normal approximation of the binomial distribution and compute the following z test statistic,

$$z = \frac{(x + .5) - np}{\sqrt{npq}},$$

which is approximately distributed as normal (0, 1) under the null hypothesis. The added .5 term is a continuity correction factor (e.g., Siegel 1956), and x is chosen to be the number of representatives of the sex having fewer individuals. The z statistics are used in conjunction with one-tailed hypothesis tests. The third type of test is used to compare sex ratios of two samples. Here we employ the χ^2 contingency test computed in the usual manner.

RESULTS

Table 1 summarizes available data on sex ratios of alligators, and includes six samples from wild populations in southwestern Louisiana and two samples from a Louisiana "farm" population. The samples have been subjectively classified according to how representative they are of their corresponding populations. Data from the 1972 and 1973 Louisiana experimental harvest seasons are known to be nonrepresentative because of harvest regulations designed to select males (Palmisano et al. 1973; Joanen et al. 1974). The exact collecting procedures of O'Neil (1949) are not known, although we have no reason to suspect that his samples are not representative of the studied population. Our own data from a wild population were not restricted to a particular habitat and are believed to be representative, as are the farm samples (R. Kliebert, personal communication), which were made up of animals randomly selected from pens. Table 1 does not include one additional reference providing alligator sex-ratio data (Forbes 1940a) because of our inability to assign the sample to a wild or farm population. Forbes (1940a) reported receiving 166 young alligators, aged 19 mo or less, from a "dealer." The sex ratio of this sample was .331 and differed significantly from .5 ($P < .001, z = -4.27$). It is not known whether these animals originated from wild eggs that had been collected and artificially incubated, or whether they were caught as young hatchlings. Forbes (1940a) also reported that the dealer, who was "believed competent

TABLE 1

OBSERVED SEX RATIOS AND CORRESPONDING TEST STATISTICS FOR ALLIGATORS FROM WILD AND "FARM" POPULATIONS†

Sample Source	Representativeness of Sample‡	Size Class§	General Age Class	No. Observed Males	No. Observed Females	Sex Ratio M/(M + F)	Test Statistic or Binomial Probability‖	Information Source
Wild populations								
1972 experimental harvest	Selective for males	1.2–1.5 m	Imm.	21	13	.617	$P(x) = 1.15 \times 10^{-1}$	Palmisano et al. 1973
		1.5–1.8 m	Imm.	55	19	.743	$z = -4.07$****	
		>1.8 m	Ad.	162	33	.831	$z = -9.17$****	
1973 experimental harvest	Selective for males	1.2–1.5 m	Imm.	45	29	.608	$z = -1.74$**	Joanen et al. 1974
		1.5–1.8 m	Imm.	110	64	.632	$z = -3.41$****	
		>1.8 m	Ad.	404	191	.679	$z = -8.69$****	
Alligator food habits study (1941)	Not known	$\bar{X} \approx 1.8$ m	Imm. + Ad.	76	21	.784	$z = -5.48$****	O'Neil 1949
Alligator food habits study (1942)	Not known	$\bar{X} \approx 1.8$ m	Imm. + Ad.	131	97	.574	$z = -2.19$**	O'Neil 1949
Captured live and released (1959–1960)	Representative	0.6–0.9 m	Imm.	197	108	.646	$z = -5.04$****	Chabreck unpublished
		0.9–1.2 m	Imm.	455	270	.628	$z = -6.83$****	
		1.2–1.5 m	Imm.	222	193	.535	$z = -1.37$*	
		1.5–1.8 m	Imm.	66	60	.524	$z = -0.46$	
		>1.8 m	Ad.	39	18	.684	$z = -2.65$***	
Captured and necropsied (1972)	Representative	0.3–0.6 m	Imm.	13	3	.813	$P(x) = 1.06 \times 10^{-2}$**	Chabreck and Nichols unpublished
Alligator farm								
1976 harvest	Representative	1.2–1.8 m	Imm.	6	41	.128	$P(x) = 8.86 \times 10^{-10}$****	Kliebert (person. commun.)
1977 harvest	Representative	1.2–2.1 m	Imm.	70	229	.234	$z = -9.14$****	Kliebert (person. commun.)

† All data for wild populations were obtained for alligators inhabiting the coastal marshland of southwestern Louisiana. The artificially reared animals were taken from an alligator farm belonging to the Kliebert brothers near Hammond, Louisiana.

‡ "Representativeness" constitutes our subjective decision about whether the samples were representative with respect to the sex ratio of the sampled population, or whether the sampling methods were selective or biased towards one sex.

§ Alligators are generally grouped into 0.3-m size classes by total body length. We have reported wild immature (less than 1.8 m total body length) sex ratios by 0.3-m size intervals when possible, but have combined all adult size classes because adults are less relevant to our arguments. The farm animals were kept in age-specific pens and virtually all the animals reported here (with the possible exception of an occasional older animal which may have climbed into the pen, not known to have occurred) are aged 2 yr.

‖ The z statistic is computed as: $z = [(x + .5) - np]/\sqrt{npq}$ where n is total sample size, $p = q = .5$, and x is the number of males or females (whichever is smaller). The probability of obtaining x or fewer males or females (whichever is smaller) is computed as: $P(x) = \Sigma_{i=0}^{x} \binom{n}{i} p^i q^{n-i}$; $P(x)$ is computed for small samples (n < 50) and z is used for large samples. In both cases one-tailed tests are used to test the null hypothesis that sample sex ratio is .5. The alternative hypothesis is represented by an excess of males in the wild populations and an excess of females in the farm population.

* .05 < P < .10.
** .01 < P < .05.
*** .001 < P < .01.
**** P < .001.

to determine the sex of young alligators," had found two nests of 41 alligators aged 5 mo and had determined that only 11 of these animals were males. We have not included this sample in table 1 because we are aware of no method by which alligators of that age can be externally sexed (see Brazaitis 1968).

We are especially interested in making inferences about sex ratios for specific age classes, but many of the wild population data of table 1 do not permit assignment of specific age classes to size intervals. Chabreck and Joanen (1979) demonstrated that male and female growth rates began to differ significantly at a body length of 100 cm (during the third year of life). By the fourth and fifth years of life female growth rates seem to slow to the extent that the 0.3-m size intervals of animals greater than 1.2 m contain cohorts of more than one age or year class. The probable occurrence of more age classes of females than of males in the size intervals 1.2–1.5 m and 1.5–1.8 m obscures the meaning of sex ratios associated with these size intervals and assures a larger proportion of females than would be expected in a comparison of single age class samples.

In the wild populations empirical sex ratios exhibited a preponderance of males in all samples, and the test statistics permit rejection ($P < .05$) of the hypothesis of a .5 sex ratio in 11 of the 14 samples (table 1). All three of the samples for which this hypothesis could not be rejected occurred in size intervals expected to include more female than male age classes. The three samples of greatest interest from wild populations are those representing the three smallest size intervals: 0.3–0.6 m, 0.6–0.9 m, and 0.9–1.2 m, roughly corresponding to the first, second, and third years of life, respectively (Chabreck and Joanen 1979; McIlhenny 1934; Chabreck 1965). These three samples are believed to be representative, and all exhibit significantly greater proportions of males than expected under the hypothesis of a 0.5 sex ratio. We suggest that it is highly unlikely that the sex ratios in these three samples represent the results of a .5 hatching sex ratio coupled with high sex-specific mortality of females. During the first year and a portion of the second year of life, young alligators tend to remain near the hatching site and the den of the mother (Chabreck 1965; Joanen and McNease 1971). Both immature males and females would thus be exposed to the same risks and mortality factors during this period. After the first 18 mo immature alligators move about a great deal; no sex-specific differences in movement were found in the capture-recapture work of Chabreck (1965). McNease and Joanen (1974) found sex-specific differences in habitat preferences of immature alligators, but these animals ranged from 0.9 m to 1.8 m total body length and were probably all older than 2 yr. At this age alligators are relatively free from predation. The similar growth rates of alligators during the first 2 yr of life (Chabreck and Joanen 1979) suggest similar patterns of energy allocation and again provide no evidence of differential mortality during this period. We conclude from our samples and these tests that the proportion of males among very young alligators appears to be significantly greater than .5 in wild alligator populations.

The 1976 and 1977 samples of 2-yr-old farm alligators included very high proportions of females (table 1). In both samples, the hypothesis that sex ratio was .5 was conclusively rejected ($P < .001$). Total mortality from hatching to age 2 yr in these animals averaged 5% (R. Kliebert, personal communication). Even if all

of this mortality was concentrated on males (there was no evidence of differential sex-specific mortality), the hatching sex ratio (if sex had been determined at that time) would have still been significantly lower than .5. We conclude that sex ratio of these young farm alligators was lower than .5, and that differential sex-specific mortality rates after hatching coupled with a .5 hatching ratio could not have produced so extreme a result.

The wild and farm population samples appeared to exhibit strikingly different sex ratios, and we were interested in testing the hypothesis that sex ratios from samples of comparable age were different. The 0.9–1.2-m size class of wild-captured animals consisted primarily of 2-yr-old individuals (see Chabreck and Joanen 1979; McIlhenny 1934; Chabreck 1965). This sample of 725 individuals was compared with the combined farm sample of 346 animals (also 2-yr-olds) using a 2×2 χ^2 contingency test. The sex ratios of the two samples were concluded to be significantly different ($P < .001$, $\chi^2 = 155.9$, 1 df).

DISCUSSION

We have thus concluded that sex ratios of very young alligators from both the farm and wild populations differed significantly from .5, a result which is somewhat unusual for vertebrates. Even more interesting is the significant difference between sex ratios of the two large samples of 2-yr-olds, with males predominating in the wild population and females in the farm population. This latter difference leads us to suspect environmental influence on the mechanism of sex determination in alligators. The farm alligators originated from clutches of wild-caught animals kept in large enclosures at Kliebert's "farm." The newly hatched alligators were transferred to tanks that were heated in winter months (wild animals become semidormant during cold weather), and were fed generously to induce rapid growth. This treatment produced 2-yr-old animals that were considerably larger than most animals of similar age in wild Louisiana populations (see Coulson et al. 1973 for similar growth rate results). Thus the environments in which the two groups of young alligators were reared were markedly different. Sex chromosomes have not been found in alligators (Risley 1942; Cohen and Gans 1970) or, for that matter, in crocodilians as a group (Becak et al. 1964; Ohno 1967; Cohen and Gans 1970). While we realize that this does not exclude the possibility of chromosomal sex determination, the apparent lack of such a mechanism supports the feasibility of some environmentally influenced mechanism. It is also pertinent that young alligators exhibit aspects of bisexuality. In numerous (80+) dissections of newly hatched alligators (J. D. Nichols and R. H. Chabreck, unpublished) we have consistently noted the presence of both Wolffian and Mullerian ducts (the embryonic precursors of sperm ducts and oviducts, respectively). Bisexual aspects of young alligators have also been reported and described by Forbes (1938, 1940b, 1940c). Thus, we suspect that alligator sex may not be rigidly determined by the time of hatching, and may be influenced by the posthatching environment.

T. Joanen (personal communication) has suggested that alligator hatching sex ratio may be influenced by incubation temperature. Yntema (1976) has presented convincing evidence regarding effects of incubation temperature on sexual differ-

entiation in the snapping turtle, *Chelydra serpentina*, and such effects could be important in alligators. Incubation temperatures were not measured for the farm alligators, and it is possible that they deviated to some extent from those common to wild alligator nests (see Chabreck 1973 for data on incubation temperatures of wild alligators). It is difficult to envision the adaptive significance of a sex ratio which varies with incubation temperature, unless perhaps temperature influences growth rate and thus size or physiological condition of hatchlings. In any case, we have no evidence indicating any influence of incubation temperature on alligator sex ratio and thus suspect that sex ratio is influenced by the posthatching environment, as suggested earlier. However, we cannot dismiss the incubation temperature hypothesis as a possibility.

Regardless of the actual mechanism of sex determination, we would like to use the observed pattern of variation in sex ratios of young alligators to test the generality of recent hypotheses dealing with the evolution of variable sex ratios and environmental sex determination (Trivers and Willard 1973; Charnov and Bull 1977). Charnov and Bull (1977) have suggested that environmental sex determination should be most strongly favored by selection in cases where the environment is variable or patchy with respect to the relative advantage of being male or female, and where there is little control exerted by parent or offspring over which patch type the offspring enters. There are certainly differences in the microhabitats in which hatchling alligators find themselves, depending, for example, on whether the nest is located on a levee or ridge, along a large water body, or in the interior marsh. However, adult female alligators do exert control over this source of variation via nesting habitat selection (see Joanen and McNease 1970). The Louisiana coastal marsh also exhibits temporal variation with both food resource abundance and hatchling mortality risks due to predation and desiccation, apparently varying in response to year-to-year changes in marsh water levels. Nesting female alligators can exhibit only limited control over such variation in habitat suitability (some control is possible through the "decision" not to nest in especially dry years).

Thus, the conditions predicted by Charnov and Bull (1977) to favor the evolution of environmental sex determination (environmental patchiness and relative lack of control over patch type encountered by offspring) seem to be met by the alligator. However, Charnov and Bull (1977) and Trivers and Willard (1973) predict not only environments that are patchy but environments that are patchy with respect to the relative advantage of being male or female. We have noted that the alligator's environment varies temporally with respect to resource abundance and hatchling mortality. Because of the similarity of growth rates, movement patterns, and habits of hatchling alligators, we discount the possibility of sex-specific mortality differences at this age. Werren and Charnov (1978) present a "perturbation model" suggesting that differential sex-specific responses to periods of exceptional mortality or survival can result in selection for the temporary overproduction of one sex. However, the perturbation model of Werren and Charnov (1978) essentially involves a "prediction," by either reproducing females or new young, of the adult sex ratio expected to exist when the young reach sexual maturity. Such predictions would probably be unreliable in a species like the alligator, which exhibits a long development time. For these reasons, and because

of the fact that the major difference between the "farm" and natural environments involved resource abundance, we feel it is most reasonable to look for differences in the value of resources to males and females when seeking an explanation for the observed sex-ratio differences.

Trivers and Willard (1973) argued that, in species in which parental investment by males is negligible, selection should favor the production of males during periods of resource abundance. This prediction follows from the assumption that in such species reproductive success of males is expected to vary more than that of females (Trivers 1972). Thus, any early advantage (obtained either from being born to a female in good physical condition or from experiencing resource abundance during early growth) that is maintained until adulthood should have greater effects on male reproductive success because of the importance of competition for females and the ability of superior males to inseminate many females (Trivers and Willard 1973). In adult male alligators parental investment is certainly negligible, and males possess the ability to inseminate several females per breeding season (Chabreck 1965; Joanen and McNease 1975). Competition for mates is important, as evidenced by fighting between males during the breeding season and the establishment of mating territories (Joanen and McNease 1975; Garrick and Lang 1977). In addition, the probability of breeding is greater for males larger than 2.7 m total body length (Joanen and McNease 1975). Following the arguments of Trivers and Willard (1973), we might thus be led to predict a preponderance of males among young hatchlings in times of resource abundance. Similarly, if sex-specific differences in size reflect the relative importance of size to male and female fitness (Charnov and Bull 1977), then we would again predict a higher proportion of males (the larger sex in adulthood) among alligators when resources are abundant. However, in the farm population resources were superabundant for both parent and offspring alligators, and yet an extreme abundance of females was produced.

Although the empirical evidence on alligator sex ratios initially appears to falsify the hypotheses of Trivers and Willard (1973) and Charnov and Bull (1977), we will consider another interpretation which seems consistent with their predictions. It appears that sexual maturity in alligators is dependent on size rather than age (see Whitworth 1971; Joanen and McNease 1975). Whitworth (1971) reported obtaining a female alligator 0.3 m long (probably 1 yr old). The animal exhibited an extremely high growth rate in captivity, and mated, nested, and produced eggs 3 yr later (Whitworth 1971), at an age several years younger than the normal age of sexual maturity in the wild. It thus appears that age of first nesting may vary several years in alligators and that environmental factors and resource abundance may exert considerable influence on this age (see also Joanen and McNease 1975). If sexual maturity in alligators is a function of size and physical condition, rather than age, then a female with a high growth rate in early life could gain a substantial increase in fitness relative to other females. The fact that dramatic increases in population or genotypic rates of increase can be achieved by reductions in development time (i.e., a decreased age of sexual maturity) is well known to ecologists (e.g., Cole 1954; Lewontin 1965), and could result in large differences in fitness between fast- and slow-maturing females.

These postulated differences in female fitness do not lead us directly to the

prediction of low sex ratios in times of resource abundance. Male alligators also exhibit high growth rates during periods of resource abundance and must experience increases in relative fitness because of larger size and associated reproductive advantages (as discussed earlier), as well as increases because of possible reductions in development time. Reproductive success of males or females relative to members of the same sex must be a function of age at first reproduction, age-specific (or size-specific) probabilities of breeding and successfully producing young, and age-specific (size-specific) survival probabilities. There is simply not enough information available on alligators to compute adequate measures of relative lifetime reproductive success for varying levels of resource abundance. However, we have suggested a source of variation in female reproductive success (via the postulated functional relationship between resource abundance and age at sexual maturity) which may be of sufficient magnitude to produce large differences in relative fitnesses of females. We further suggest that these differences may be larger than those experienced by males at varying resource levels. In addition, as an anonymous reviewer pointed out to us, the relative fitness gain associated with a decreased age of sexual maturity is probably more predictable for females than males. Even after reaching reproductive size, males must still compete for females. This factor should result in lower predictability of relative fitness gains for young males experiencing high resource levels. In any case, we suggest that the differences in female fitness associated with different ages of sexual maturity could reconcile our empirical results with the generalized predictions of Trivers and Willard (1973) and Charnov and Bull (1977).

Corroboration for the relationships we have hypothesized comes from a large scale rearing experiment involving another reptile, the diamond-back terrapin (*Malaclemmys centrata*), in which a marked preponderance of females (sex ratio = 0.14, n = 1,433 animals) was produced (Hildebrand 1932, 1933). Growth rates of these animals were increased through winter feeding, and sexual maturity in this species was shown to be a function of size rather than age (Hildebrand 1932, 1933). Hildebrand's data came from broods (groups of clutches) produced annually for over a decade. The annual brood exhibiting the lowest age of sexual maturity (the 1911 brood was fed three winters and produced eggs when 4 yr old) was also the brood with the most disproportionate sex ratio (148 females and no males; Hildebrand 1932). The brood that required the longest time to reach sexual maturity (the 1919 brood was fed only one winter and produced eggs at age 8 yr) was the brood with the highest sex ratio (93 females and 54 males; Hildebrand 1932). These extremes in sex ratio and age at maturity thus correspond closely to our predicted relationship between these two parameters.

SUMMARY

Samples of alligators from wild and "farm" populations exhibited disproportionate sex ratios. Males predominated among young alligators from wild populations, whereas females were much more abundant than males in the farm population, where resources were superabundant. These results and other considerations lead us to hypothesize that environmental factors influence sex

determination in alligators. During favorable environmental conditions natural selection is expected to favor a preponderance of the sex whose individuals exhibit the greater environmentally associated variation in relative fitness. We hypothesize that environmentally associated variation in age at sexual maturity of females produces sufficient variation in relative fitness of females to result in selection for low sex ratios during periods of resource abundance.

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