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Enigmatic reptilian sex ratios

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ular case [see Warner and Hoffman (1980) for a test of Eq. (1) in some particular cases].

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ENIGMATIC REPTILIAN SEX RATIOS

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When confronted with the academic question of sex-ratio evolution, the untrained person typically supposes that natural selection favors a female excess in the population. However, research spanning half a century has led sex-ratio experts to conclude that a female excess is favored only under unusual circumstances. An objective evaluation of sex ratios in reptiles with environmental sex determination offers the humbling prospect that the nonexperts are closer to the truth. The failure of sex-ratio theory to explain reptilian sex ratios stands in sharp contrast to its empirical success in other groups and thus warrants special attention.

The unexplained sex-ratio phenomena in reptiles come chiefly from species with temperature-dependent sex determination: incubation temperature determines whether embryos hatch as male or female in perhaps all crocodylians, many turtles, and at least a few lizards

(Bull, 1980; Raynaud and Pieau, 1985). Two problems arise in understanding sex-ratio evolution in these systems. First, there is no clear advantage of environmental sex determination. Second, the primary sex ratio of many species heavily favors females (reviewed in Bull and Charnov [1988]). Here, we illustrate how sex-allocation theory addresses each of these problems, and we discuss empirical evidence in light of the relevant models.

Hypotheses for Evolution of Environmental Sex Determination and a Skewed Primary Sex Ratio

Charnov and Bull (1977) proposed a model to explain the evolution of environmental sex determination which assumes that sex is determined in response to an environmental factor differentially influencing

fitness as male versus female. That model provides the foundation for the analysis here. Define variables as follows:

- t = the environmental determinant of sex (e.g., egg temperature), distributed as a continuous variable
- r = the primary (1°) sex ratio among all progeny in the population, calculated as the proportion male that would be observed at any stage of the life history if all conceived progeny survived to be counted
- $W_m(t)$ = "fertility" of an individual exposed to t if it develops as male, defined as the expected lifetime fitness of a male (exposed to t) divided by the fitness of a standard male
- $W_f(t)$ = the corresponding fertility as female, relative to a standard female
- \bar{W}_m = the average male fertility over the population of males
- \bar{W}_f = the average female fertility over the population of females.

We imagine that each individual is exposed early in life to an environment whose attributes include some value of $t = T$. Its lifetime fertility is $W_m(T)$ if it becomes male, $W_f(T)$ if it becomes female. All "fertilities" $W_m(t)$ and $W_f(t)$ are measured as fitnesses divided by the fitness of an arbitrarily chosen individual of the same sex; because of this scaling, fertilities do not vary with sex ratio and do not equal total fitness. We consider randomly mating populations, and aside from the possible fitness effects of t , the assumptions underlying this model are the same as those underlying Fisher's (1930) model of sex-ratio evolution for the special case that the cost of a son equals the cost of a daughter (cf. Bull and Charnov, 1988).

The Form of Environmental Sex Determination.—Under these assumptions, environmental sex determination evolves as an individual's response to t in developing as male or female, and the form of environmental sex determination favored is readily anticipated from the ratio $W_m(t)/W_f(t)$. When the sex-ratio response has evolved to its evolutionarily stable form, there will be some threshold value of this ratio (V), such that only males develop at values of t for which this ratio exceeds V and only females develop at values of t for which this ratio is less than V ; the value of V depends in a complicated manner on the distribution of t and on the fitness functions $W_m(t)$ and $W_f(t)$. For $W_m(t)$ and $W_f(t)$ of biological interest, there will be at least one value of t (designated as $t = \tau$) such that $W_m(\tau)/W_f(\tau) = V$. The evolutionarily stable form of environmental sex determination will change from all one sex to all the other sex at τ (referred to as a sex-determination threshold). In principle, there is no limit to the possible number of such thresholds. In summary, therefore, environmental sex determination is favored whenever t differentially influences male and female fertility, so that the ratio $W_m(t)/W_f(t)$ varies with t (Charnov and Bull, 1977; Charnov, 1979; Bull, 1981).

Population Primary Sex Ratios.—The equilibrium primary sex ratio among all offspring does not generally obey Fisher's sex-ratio equilibrium of $1/2$, but it instead satisfies the following rule:

$$\frac{1}{\hat{r}} \frac{W_m(\hat{r})}{\bar{W}_m} = \frac{1}{1 - \hat{r}} \frac{W_f(\hat{r})}{\bar{W}_f} \quad (1a)$$

or

$$\frac{\hat{r}}{1 - \hat{r}} = \frac{\frac{W_m(\hat{r})}{\bar{W}_m}}{\frac{W_f(\hat{r})}{\bar{W}_f}} \quad (1b)$$

where carats indicate values taken at an evolutionarily stable equilibrium (Charnov, 1982; Frank and Swingland, 1988; Charnov and Bull, 1989a). Equation (1a) equates the total fitness of a male and female raised at $t = \hat{r}$. The terms $1/\hat{r}$ and $1/(1 - \hat{r})$ represent the Fisherian, frequency-dependent components of selection that, by themselves, select a primary sex ratio of $1/2$. The factors $W_m(\hat{r})/\bar{W}_m$ and $W_f(\hat{r})/\bar{W}_f$ are therefore the basis of non-Fisherian sex ratios in this model. Each ratio is the fertility of an individual raised at \hat{r} relative to the average fertility for its sex. Their inclusion into the sex-ratio equation can be understood by noting, for example, that if some individuals are born at values of t enabling them to become males of above-average fertility or females of average fertility, selection clearly favors development as males under these circumstances (aside from sex-ratio considerations; cf. Trivers and Willard, 1973; Charnov and Bull, 1977). Recalling that \hat{r} is a value of t at which the sex ratio changes from all-male to all-female (at sex-ratio equilibrium), it is necessarily also a value at which the fitness of an individual is independent of its sex, hence the equality in (1a). It is thus apparent that non-Fisherian sex ratios arise in this model from fitness effects of t within a sex.

Equation (1) is useful in that it describes the minimum magnitude of environmental effects on fertility required to maintain a skewed primary sex ratio. An equilibrium sex ratio of $1/2$ requires that the relative fertility of a threshold male be half that of a threshold female. In some cases, the relative magnitudes of $W_f(\tau)/\bar{W}_f$ and $W_m(\tau)/\bar{W}_m$ can be anticipated trivially from knowledge of $W_m(t)$, $W_f(t)$, and the distribution of t , in which case a male excess or a female excess can also be anticipated. In other cases, these magnitudes will not be so obvious, and it will be difficult to predict even the direction of sex-ratio skew without detailed calculations. In particular, one cannot predict whether males or females should predominate at equilibrium merely by knowing the form of environmental sex determination: the primary sex ratio depends on the ratios $W_m(\tau)/\bar{W}_m$ and $W_f(\tau)/\bar{W}_f$, whereas the form of environmental sex determination depends on $W_m(t)/W_f(t)$ across t (Charnov and Bull, 1989a).

In species with environmental sex determination, the hatchling or secondary (2°) sex ratio may be more easily observed than the primary sex ratio. Under reasonably general conditions, a skewed secondary sex ratio contains information about the average post-hatching fertility effects of t . Define an individual's lifetime fertility as the product of two functions: survival from conception to hatching, $s(t)$, and posthatching fertility, $W'_m(t)$ for males and $W'_f(t)$ for females. The equilibrium sex ratio among surviving hatchlings, \hat{R} , obeys the rule

$$\frac{\hat{R}}{1 - \hat{R}} = \frac{\frac{W'_f(\hat{r})}{\bar{W}'_f}}{\frac{W'_m(\hat{r})}{\bar{W}'_m}} \quad (2)$$

TABLE 1. Sex ratios reported in reptiles with environmental sex determination. Stage of life history at which the sex ratio was measured: 1° = primary sex ratio (of nests); 2° = secondary (of hatchlings). The sex ratio here is the proportion male, usually rounded to the nearest 0.1. Values obtained from different studies for a single species have been averaged in most cases. Original references and comments on the data were provided in Bull and Charnov (1988), except for the study of Mrosovsky and Provancha (1989), which reports a sex ratio of 0.1 in loggerhead sea turtles.

Reptile	Sex ratio	Life-history stage	Sex-determining temperatures	
			Male	Female
Crocodylians				
Alligator	0.2	1°, 2°	warm	cool
Freshwater crocodile	0.35	2° ^a	intermediate	hot and cold
Turtles				
Loggerhead sea	0.1, 0.5	1°	cool	warm
Green sea	0.3, 0.5	1°	cool	warm
Leatherback sea	0.5	1°	cool	warm
Snapping	0.3	1°	intermediate	hot and cold
Map	0.35	2°	cool	warm

^a The primary sex ratio is apparently even more skewed toward females, but the magnitude is unknown.

If all fertility effects of temperature are manifested in survival to hatching, the equilibrium secondary sex ratio is $\frac{1}{2}$. We emphasize that (2) does not apply if male and female embryos exposed to the same value of t survive to hatching at different rates, but available data do not offer much insight concerning the plausibility of this assumption.

The arguments in this section have incorporated the Charnov-Bull framework. Sex-allocation theory provides alternative models to account for non-Fisherian sex ratios and for the maintenance of environmental sex determination (see general treatments by Charnov [1982], Bull [1983], and Karlin and Lessard [1986] and a special model proposed by Huey [1982]). Our focus on one model should not be construed as an unwillingness to consider alternatives. Rather, despite the fact that the Charnov-Bull model has been the focus of most recent attempts to understand the evolutionary significance of environmental sex determination (Conover and Heins, 1987; Naylor et al., 1988; Deeming and Ferguson, 1989; Webb, 1989), there has not been a succinct presentation of its joint implications to the evolution of environmental sex determination and population sex ratios, which is our objective here.

Observed Sex Ratios

Primary and secondary sex ratios reported from reptile populations with environmental sex determination are consistent with $\frac{1}{2}$ or favor females (Table 1). The studies vary in the degree to which collections necessarily reflect population-wide sex ratios, but at least some studies appear to be relatively free of such problems, and extreme female excesses are reported for these species as well: the crocodylians and snapping turtles (summarized in Bull and Charnov [1988]; see also Mrosovsky and Provancha [1989]).

The sex ratios are no more skewed in these reptiles than in other species with environmental sex determination or in sex-changing species, and (1) appears to explain the skews in these other cases (Charnov and Bull, 1989b). Yet the success of (1) in these other species lends no credibility to the model's validity with rep-

tiles. These nonreptilian examples all involve species in which life-history considerations suggest that a large portion of the population experiences values of t that yield low fitnesses, and these fitness considerations in turn are consistent with the direction of observed sex-ratio skews.

In reptiles, however, there is no basis for arguing that nests are often laid at t values so extreme as to induce major fitness decrements. It is indeed true that incubation temperature per se can affect embryonic survival (Gutzke and Packard, 1985; Webb and Smith, 1984; Webb, 1989; Yntema and Mrosovsky, 1980), but there are few reports on the extent to which temperature might directly influence survival in natural nests (Webb [1989] is exceptional in reporting that temperature per se is a leading cause of natural embryonic mortality). Of greater concern, perhaps, is the possibility that nest temperature might be correlated with some common cause of nest mortality. For example, cool nests slow embryonic development and may enhance exposure to lethal factors such as flooding (Webb, 1989; Webb and Smith, 1984) or failure to hatch before winter (Bull, unpubl. [observations on map turtles]).

Empirical estimates are not available on the magnitudes of these effects in natural populations, but even in the absence of such estimates, theoretical arguments call into question whether the choice of grossly suboptimal t values would persist under natural selection: nest site is a consequence of maternal behavior, and mothers are potentially capable of avoiding values of t that yield low offspring fitness (Schwarzkopf and Brooks, 1987; Bull et al., 1988). At the evolutionarily stable equilibrium for unconstrained female choice of t , any association between t and fitness within a sex should vanish, yielding a sex-ratio equilibrium of $\frac{1}{2}$ (Bull, 1981); this result holds whether the fitness effects of t are frequency-dependent or frequency-independent and with density-dependent or density-independent female choice of t (the use of suboptimal t is expected if there is any cost to female choice of nest sites).

Of course, a mother's lifetime reproductive success depends on the number of clutches she produces as well as on average clutch fitness, and her total reproductive success may be maximized by compromising clutch fitness to increase clutch number. It is difficult to anticipate the covariance between t and offspring fitness that would stem from these constraints, but it should be possible to conduct field studies to obtain this information. Reptilian nests typically experience substantial levels of mortality, so it should be feasible to determine whether nest mortality is correlated with t and whether the primary sex ratio is skewed in the corresponding direction. Nest mortality cannot account for skewed secondary sex ratios, but if it is generally found that primary and secondary sex ratios favor the same sex, the possibility should be entertained that prehatching survival effects of t are correlated with posthatching survival or fertility effects. In fact, Webb (1989) provided the first analysis of pre- and posthatching effects of temperature on survival, and inspection of the data suggests that the two effects may be correlated.

Why Environmental Sex Determination?

The very existence of temperature-dependent sex determination in reptiles also poses an evolutionary dilemma. Models indicate that temperature-cued environmental sex determination will be favored if incubation temperature has different fertility consequences for males than for females (Charnov and Bull, 1977; Bull, 1981). Environmental sex determination is selected against if between-year fluctuations in the environment generate sex-ratio fluctuations, and as fluctuations of this sort would seem to be unavoidable, it may be concluded that environmental sex determination will be maintained only if it has a compensating advantage (Bull, 1981).

A major empirical question is thus whether incubation temperature has differential effects on male and female fertility in reptiles consistent with the requirements of the model. Two lines of inquiry have been proposed: i) direct measure of temperature effects on development and ii) a search for patterns between life-history characteristics and the form of environmental sex determination. The direct approach has yielded several demonstrations that temperature and other incubation conditions affect morphology, physiology, and behavior at hatching (Packard and Packard, 1986; Miller et al., 1987; Gutzke and Packard, 1985; the evidence on crocodylians was reviewed by Webb [1989]). A few studies have investigated whether effects of incubation temperature persist beyond hatching, with mixed success. In some cases, no such effect was detected (Bull and Licht, unpubl. [observations on male *Trachemys scripta* turtles]); in others, temperature was shown to have an effect beyond hatching (Lang, 1987 [behavior]; Hutton, 1987 [growth]; Webb, 1989 [growth and survival]), but information was not provided on whether the effect was similar in males and females, and few studies have been careful to separate the potentially confounding effects of incubation temperature and sex. In some cases, an effect of temperature has been shown to persist beyond hatching and to influence males differently than females (Joanen et al., 1987 [growth]; Gutzke and Crews, 1988 [behavior and hormone levels]). Of course, an effect of temperature with the

same phenotypic effect on males as on females could have different fitness consequences for the two sexes.

These direct approaches to this problem have involved rearing reptiles from hatching to adult, so that adult phenotypes can be correlated with incubation histories. The obvious difficulty with this work is that it is impractical to rear large numbers of reptiles for the duration of their immature lifespan. Understanding the long-term effects of incubation temperature would be greatly facilitated if adults could be assayed directly for indicators of their embryonic incubation history. This approach has not been explored in reptiles, but such methods might derive from differential incorporation of isotopes in calcareous structures (Mook and Vogel, 1968; Burk and Stuiver, 1981) or from physiological processes of the adult that mirror incubation temperatures experienced as an embryo (cf. Webb et al., 1987; Gutzke and Crews, 1988).

"Comparative" approaches offer the possibility of discovering a selective advantage of environmental sex determination merely by contrasting the life histories of species with different forms of environmental sex determination. In reptiles, three patterns of environmental sex determination are observed: I) males develop at low temperatures, females at warm ones; II) the reverse of pattern I; III) males develop at intermediate temperatures, females at cool and warm extremes (Bull, 1980; Mrosovsky, 1980; Lang and Whitaker, 1989). According to our model, the benefit of warm versus cool temperatures to male and female fertility must be reversed between patterns I and II, and these benefits should differ yet from those under pattern III.

Pattern I occurs in many turtles, pattern II occurs in some lizards and alligators, and pattern III exists in crocodiles of the genus *Crocodylus* and in some turtles. Bull (1983 p. 141) was unable to find any associations between these patterns of environmental sex determination and life histories that might suggest an advantage of environmental sex determination. Head et al. (1987) suggested that pattern I occurred in species for which females were larger than males whereas species with pattern II had the reverse sex dimorphism, and they suggested that the advantage of environmental sex determination arose from temperature effects on growth, because faster growth is relatively more beneficial to the larger sex. The analysis was flawed by failing to account for taxonomic biases and failing to note some obvious exceptions to the pattern (e.g., tortoises [Berry and Shine, 1980; Raynaud and Pieau, 1985]), but the attempt nonetheless leads one to consider models of similar vein, some of which may yield new insights. A full analysis of the Head et al. (1987) hypothesis is being developed by F. Janzen and G. Paukstis.

Recent results have injected an air of optimism toward understanding the possible sex-specific fitness effects of temperature in reptiles. Most suggestions have centered around the possibility that incubation temperature affects posthatching growth, translating into different fitness consequences for males than for females (first proposed by Ferguson and Joanen [1982]; generalized by Deeming and Ferguson [1989]). Optimism on this problem stems from an otherwise total failure for nearly a decade to understand why environmental sex determination might be favored in reptiles, and although continued research on the problem is to

be encouraged, there are several questions to be addressed before one can accept any general model of temperature effects on growth as the basis for environmental sex determination in reptiles.

i) *Does enhanced posthatching growth lead to earlier maturity or larger adult size?*—Earlier maturity is likely to benefit the sex maturing first (i.e., the smaller sex), because a year's advancement to maturity has a proportionately bigger impact on a small number than on a big number. Alternatively, larger adult size might differentially benefit the larger sex. The ultimate effect of enhanced growth must thus be understood before it can be predicted which sex benefits more. The only relevant study known to us compared growth of diamond-backed terrapins fed during their first winter of life with growth of terrapins hibernated during their first winter: the turtles matured a year earlier if they fed during their first winter, but no ultimate size difference between the two groups was found (Hildebrand, 1929).

ii) *Does temperature affect growth rate or just influence the starting point, such that some individuals have a headstart?*—If the latter applies, then it is difficult to understand why other headstart factors, such as egg size and water potential, do not also have major effects on sex.

iii) *How general are the effects of temperature on growth?*—Environmental effects on growth are notoriously elusive. In mammals, the phenomenon of catch-up growth compensates for early periods of low nutrition, so that embryos from widely differing environmental conditions are born at nearly the same size (Pitts, 1986). Do reptiles exhibit a similar phenomenon? Once again, the data of Hildebrand (1929) are interesting: a group of 800 yearling terrapins were divided into 100 of the smallest individuals and 100 of the largest individuals; the average carapace length of the group of smaller turtles was 32.3 mm and that of the larger group was 65 mm some six months after the separation. Within three years, the size differential between the groups had reversed, a reversal that persisted until the end of the study a decade later. Thus, short-term studies of posthatching growth may give misleading results about adult sizes. In a similar vein, Webb et al. (1987) pointed out inconsistencies in the data that frustrated generalizations about temperature effects on crocodilian hatchlings, but generalizations do seem to be emerging with respect to temperature-effects on posthatching growth (Webb, 1989).

One wonders, in fact, whether the emphasis on temperature effects on growth has been premature, and that other general effects of incubation temperature on reptilian fitness remain to be discovered. The recent discoveries of possible incubation-temperature effects on behavior mentioned above offer one of the few demonstrated alternative avenues of study, and those interesting results highlight the benefit to be gained from broadening the search for incubation-temperature effects on adult phenotypes.

In conclusion, the female excess in reptiles with environmental sex determination and the existence of environmental sex determination itself have not been satisfactorily explained. Although the Charnov-Bull model is not yet supported by the data, it is also not evidently inconsistent with the data either. The main difficulty in testing this model with reptiles is that its

success depends on the existence of particular types of long-term fitness effects correlated with incubation temperature, and conclusive data will not be easily obtained unless large fitness effects of incubation temperature exist. The observed sex ratios in these reptiles offer some hope that such fitness effects may indeed be large.

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