"The Adaptive Significance of Temperature-Dependent Sex Determination in a Reptile" (2008), by Daniel Warner and Richard Shine [1]

By: Moeller, Karla Keywords: Charnov-Bull model [2] Daniel Warner [3] Richard Shine [4]

In 2008 researchers Daniel Warner and Richard Shine tested the Charnov-Bull model by conducting experiments on the Jacky dragon, *(Amphibolurus muricatus)* [5] in Australia. Their results showed that temperature-dependent sex determination [6] (TSD) evolved in this species as an adaptation to fluctuating environmental temperatures. The Charnov-Bull model, proposed by Eric Charnov and James Bull in 1977, described the evolution [7] of TSD, although the model was, for many years, untested. Many reptiles and some fish [8] exhibit non-genetic sex determination [6], in which an embryo's environment can influence the sex of the adult organism. Environmental conditions such as humidity or population density can alter sex in some organisms, and a widespread form of non-genetic sex determination [6] is temperature-dependent sex determination [6]. TSD reveals how embryonic development can contribute to the evolution [7] of physiological processes. Researchers have documented TSD in a wide range of species, and they continue to investigate how such a sex determining system has evolved.

Eric Charnov and James J. Bull, then at University of Utah, in Salt Lake City, Utah, proposed the Charnov-Bull model in 1977. Richard Shine began working with Bull during his doctoral studies in the 1970s, and he later became a postdoctoral researcher in Charnov's lab from 1976 to 1978. He then became a professor at the University of Sydney in Sydney, Australia. Daniel Warner earned his doctorate while working in Shine's lab in 2007, and later became a postdoctoral researcher at Iowa State University in Ames, Iowa. Warner and Shine published "The Adaptive Significance of Temperature-Dependent Sex Determination in a Reptile" in 2008. In the article, Warner and Shine describe the results from the first empirical test of the Charnov-Bull model. Their study validated the Charnov-Bull model, showing that for some species and taxonomic groups, differential fitness may be a primary force in the evolution [7] of TSD.

According to the Charnov-Bull model, for TSD to evolve, the same environmental conditions must influence male and female reproductive success (fitness) differently. For example, females may benefit more than males from a warmer developmental temperature that causes the clutch of eggs to hatch earlier than normal. Young females that are larger than normal at the end of their first reproductive season may be able to lay eggs in their first year of life, thus increasing their reproductive potential compared to the females that do not lay eggs in their first year of life. Young males that are larger than normal may still not be large enough to compete against other males, thus the increased temperature of development would not alter their reproductive success. In this example, the reproductive success of each sex should be maximized at different temperatures, which would favor natural selection [9] for TSD.

Few tests of the Charnov-Bull model occurred prior to 2008 for at least two reasons. First, researchers had to test the reproductive success of one sex at temperatures that naturally produce that sex in the wild, as well as at temperatures that produce the opposite sex. In species for which the development of sex organs depends on the temperature of the environment, it is difficult to produce both sexes at temperatures that would naturally only produce one sex. However, using hormonal manipulations, Warner and Shine were able to produce males at temperatures that would naturally produce females, and vice versa.

Second, researchers had to develop methods to measure reproductive success for species with TSD. Reproductive success is a measure of the number of offspring produced by an individual that survives long enough to reproduce. Researchers take this measurement over the lifetime of an organism by calculating its reproductive success each year. Researchers must also measure the survival of that individual's offspring to sexual maturity. The work involved for researchers increases with the length of an organism's life, as researchers must account for reproductive success each year, and they must follow offspring from each year. Because most reptile [10] species that exhibit TSD live for more than a decade, researchers struggle to measure the reproductive success of these organisms. However, in 2000, researchers discovered that a lizard native to Southeastern Australia, called the Jacky dragon, lives only three to four years and exhibits TSD. This discovery made measurement of lifetime reproductive success for a vertebrate species with TSD more feasible.

In TSD of Jacky dragons, temperature can influence the development of sex in an embryo by regulating production of hormones [11] responsible for the development of sex organs. Specifically, the enzyme aromatase aids in the conversion of male sex hormones [12] to female sex hormones [12] and is released in higher levels at certain temperatures. During normal development, the sex hormone [13] testosterone is present in high concentrations and the standard sex produced is male, unless aromatase helps convert the testosterone into the sex hormone [13] estradiol [14] at temperatures that produce females. To manipulate this process, Warner and Shine administered an aromatase inhibitor to half of their developing Jacky Dragon eggs to counteract the feminizing effects of temperature and to ensure that the treated eggs would become male, even at temperatures that normally produced females.

Jacky dragon females are mainly produced at temperatures that are low (23 to 26 degrees Celsius) or high (30 to 33 degrees Celsius), with an even sex ratio produced at 27 degrees Celsius. Males develop mostly at intermediate temperatures (27 to 30 degrees Celsius), though the production of each sex transitions gradually between temperatures, creating some variability. In 2003, Shine and Warner divided 221 Jacky dragon eggs among three incubation temperatures: 23, 27, and 33 degrees Celsius. The intermediate temperature normally produces fifty percent females, and the extreme temperatures produce all female offspring. Half of the eggs in each treatment received an aromatase inhibitor, which successfully produced males in all treatments.

Eggs from all treatments hatched between January and March of 2004 and the researchers raised the males and females together in field enclosures for three and a half years. Researchers counted, collected, and incubated second generation eggs across all years, recording which females bore which eggs, and taking tissue samples from each offspring for paternity analyses. Paternity assignment allowed researchers to calculate male reproductive success, which is the number of offspring from a male that survive to the next year.

Results indicated that in the second season, during which most lizards became reproductive, males raised at intermediate temperatures had the greatest reproductive success of all the males, while females at extreme temperatures had more offspring than those raised at intermediate temperatures. In the third season, intermediate incubation temperatures produced the males that sired the highest number of offspring, while female reproductive success appeared unaffected by incubation temperature. Though these results varied slightly, the findings matched the predictions of the Charnov-Bull model, indicating that the reproductive success of males and females were affected differently by the same incubation temperatures.

In early 2008, *Discover Magazine's* blog, *Not Exactly Rocket Science*, and *ABC Science* featured Warner and Shine's study. In the latter news feature, Bull claimed that Warner and Shine's experiment validated the Charnov-Bull model. Warner and Shine's validation of the Charnov-Bull model emphasized that embryonic stages can influence the evolution [7] of physiological mechanisms that control the reproductive success of adult organisms.

Sources

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Subject

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- Contact Us

- The Embryo Project at Arizona State University, 1711 South Rural Road, Tempe Arizona 85287, United States
- 480.965.8927

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