

FURTHER READING

- Burnett, L. E. 1997. The challenges of living in hypoxic and hypercapnic aquatic environments. *American Zoologist* 37: 633–640.
- De Mora, S. J., S. Demers, and M. Vernet. 2000. *The effects of UV radiation in the marine environment*. London: Cambridge University Press.
- Denny, M. W. 1987. Life in the maelstrom: the biomechanics of wave-swept rocky shores. *Trends in Ecology and Evolution* 2: 61–66.
- Kanwisher, J. 1957. Freezing and drying in intertidal algae. *Biological Bulletin* 113: 275–285.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. *American Naturalist* 130: 730–757.
- Przeslawski, R., A. R. Davis, and K. Benkendorff. 2005. Synergistic effects associated with climate change and the development of rocky shore mollusks. *Global Change Biology* 11: 515–522.
- Somero, G. N. 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integrative and Comparative Biology* 42: 780–789.
- Tomanek, L., and B. Helmuth. 2002. Physiological ecology of rocky intertidal organisms: a synergy of concepts. *Integrative and Comparative Biology* 42: 771–775.
- Witman, J. D., and K. R. Grange. 1998. Links between rain, salinity, and predation in a rocky subtidal community. *Ecology* 79: 2429–2447.

SEAWEED

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SETTLEMENT

SEE LARVAL SETTLEMENT, MECHANICS OF

SEX ALLOCATION AND SEXUAL SELECTION

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The term *sex allocation* denotes the evolutionary outcome of energetic investment by individuals in sexual species when it is partitioned toward male or female function. The term *sexual selection* denotes the evolutionary process that occurs when individuals in one sex mate with disproportionate success at the expense of other individuals of the same sex.

PARENTAL INVESTMENT AND SEXUAL SELECTION

The foundation for most research on sex allocation and sexual selection is known as parental investment theory. This approach identifies a sex difference in parental investment as the source of sexual selection and as the ultimate

cause for sex differences in energy allocated toward mating effort and parental care. According to this view, males and females are defined by differences in their energetic investment in gametes. In apparent confirmation of this perspective, most sexual species exhibit gamete dimorphism, or anisogamy, in which females produce few, large ova, and males produce many, tiny sperm.

An observed sex difference in initial parental investment among species is presumed by many researchers to influence sex differences in mating and parental behavior, resulting in a taxonomic bias toward parental care in females and away from parental care in males. According to parental investment theory, not only are females, with their greater initial investment in offspring, more inclined to provide care, but the small per-gamete investment in offspring by males is presumed to predispose them to pursue opportunities for additional matings rather than care for existing young. The tendency for females to provide offspring care, according to parental investment theory, makes females a limiting resource for male reproduction, a condition that appears to explain the tendency, widely noted in scientific and popular literature, for males to compete among themselves for access to females, as well as the tendency among females to be choosy when selecting mates.

A slightly different, but still complementary perspective suggests that parental care should be provided by each sex, not according to sex differences in initial parental investment, but instead according to how such care influences each individual's future fitness. According to this optimal-fitness-returns view, it is the sex difference in expected fitness available to males and females that determines which sex provides parental care and which does not. Consistent with parental investment theory, greater expected confidence of parentage coincides with female care in most species. Unfortunately, direct tests of this and related hypotheses are complicated by difficulties researchers encounter in accurately quantifying the future fitness of individuals of either sex in natural populations.

PARENTAL INVESTMENT MEASURES OF SEXUAL SELECTION

Several parameters have been suggested for quantifying the intensity of sexual selection according to the foregoing hypotheses. The operational sex ratio ($OSR = N\delta/N\varphi = R_O = 1/R$) is based on the assumption that sexual selection results from competition among males for mates. The greater the number of mature males relative to the number of receptive females, the greater the

value of OSR becomes, and the stronger the presumed intensity of male–male competition. The sex difference in gametic investment has been quantified as the ratio of male to female potential reproductive rates (PRR). The PRR is measured by saturating individual males and females with potential partners and calculating the ratio of maximum offspring numbers produced by these individuals. The greater this ratio is, the greater the potential difference in numbers of offspring is between a maximally successful male and a maximally successful female, although no individual of either sex may achieve this potential in nature.

Both OSR and PRR are combined in Q , the ratio of males and females “qualified” to mate. Such individuals are sexually mature, have acquired reproductive resources, and are in either the “time in” or “time out” phase of their reproductive cycle. Floaters or sneakers, that is, mature individuals not currently controlling territories or resources that attract mates, are excluded from calculations of Q , whereas mature individuals, who have reproduced at some previous time but are not currently doing so, are included in this calculation.

As explained in the following sections, when some individuals mate more than once, other individuals must be excluded from mating. For this reason, any parameter that includes only mating individuals will underestimate total selection intensity. Thus, despite Q ’s synthetic concept, its policy of ignoring some classes of nonbreeding males and including others can lead to inaccurate estimates of the variance in male reproductive success and of actual selection intensity.

PARENTAL INVESTMENT AND SEX ALLOCATION

How energetic investment by parents is directed toward male and female function is the basis of sex allocation theory. The three dominant themes in this research include (1) how differential energetic investment in male and female offspring leads to deviations in population sex ratio, (2) how anisogamy influences the allocation of resources toward male or female sexual function, and (3) how opportunities for multiple mating and ensuing ejaculate competition may influence gamete number and gonadal structure.

Sex allocation theory predicts that deviations in population sex ratio will occur mainly within inbreeding-tolerant species, in which parents are expected to produce only as many sons as are necessary to fertilize the ova of these same parents’ more numerous daughters. Species exhibiting such “local mate competition” are rare in tidepools;

most populations have nearly equal sex ratios, or consist of simultaneous or sequential hermaphrodites, in which each individual represents both sexes. Because ova are presumed to be energetically more expensive than sperm, ovarian excess is expected, and is generally observed among intertidal hermaphrodites, including algae, cnidarians, flatworms, and annelids, as well as certain gastropods, crustaceans, and fish.

However, fine-scale adjustments in energetic allocation toward male or female function are also observed in hermaphrodites when sex differences in body size exist or when multiple mating, and thus sperm competition, may occur. Contrary to standard “optimal” allocation predictions, such adjustments vary widely among species and may favor male function, female function, or both sexual functions or may remain invariant for one or both functions. These results suggest a high degree of complexity in the genetic and evolutionary processes underlying the expression and persistence of sexual phenotypes; processes that are not specifically addressed, and are therefore difficult to explain, when evolutionary outcomes are emphasized.

SEX ALLOCATION AND SPERM COMPETITION

Game theory models, also known as evolutionary stable strategy (ESS) models, of sex allocation are consistent with parental investment and optimality predictions for simultaneous hermaphrodites with external fertilization. Certain polychaete worms and teleost fish, for example, show the predicted optimal bias toward female function just described. ESS models for hermaphrodites with multiple mating and sperm storage, as occurs in some polyclad flatworms and littoral gastropods, also predict a bias in energy allocation toward female function, particularly when male allocation depends on the ratio of sperm donor production to a sperm recipient’s existing sperm stores.

Yet sex allocation models that incorporate multiple mating also suggest that resources allocated toward gonads or gametes should be optimized for group size. Larger groups are presumed to permit more multiple matings and lead to increased numbers of competing ejaculates involved in each mating episode. Such apparently competitive situations are presumed by many researchers to favor individuals who allocate their energy toward sperm numbers, as well as toward male traits that facilitate sperm transfer. However, species that digest as well as store sperm, such as nudibranchs and ascidians, consistently show more equal allocation of energy toward both sexes, a result that has been attributed, not to actual ejaculate competition, but rather to avoiding the risk of ejaculate loss.

Gonadosomatic index (GSI), the ratio of gonad size to body size, is the usual measure of energetic investment in ejaculates. A large testis mass seems necessary for a high rate of sperm production, and indeed, in laboratory experiments involving gonochorists such as fruit flies, as well as hermaphrodites such as barnacles, individuals do adjust their allocation toward sperm production in response to social conditions favoring multiple mating. Although these studies are usually interpreted in light of parental investment theory, they do not directly test the central hypothesis of this approach: that initial energetic investment in sperm or ova will determine individual tendencies to emphasize mating or parental functions. The comparatively large testes of *Pseudoceros bifurcus* flatworms, for example (Fig. 1), which may engage in hypodermic inseminations of conspecifics, seem likely to have evolved as result of the differential success sperm-transferring opportunists had in siring offspring, at the expense of less aggressive inseminators. It seems less likely, as parental investment theory implies, that facultative polygamy arose in this species so that individuals with enlarged testes could capitalize on their greater initial gamete numbers.



FIGURE 1 The hermaphroditic Indo-Pacific flatworm *Pseudoceros bifurcus* engages in hypodermic insemination of conspecifics; individuals evert their penis and attempt to transfer sperm while apparently attempting to avoid being inseminated. Image by Dave Harasti, www.daveharasti.com.

A FOCUS ON EVOLUTIONARY OUTCOME

Both parental investment and sex allocation theories emphasize evolutionary outcomes; that is, they provide detailed predictions about which traits should evolve over time. There is little doubt that these solutions have significantly advanced understanding of evolution in sexual species. However, because these theoretical approaches consider “all things equal” during the evolutionary trajectories

optimal phenotypes may take, they provide few predictions about how inheritance or selection intensity may influence the evolution of sex differences or parental care. While an emphasis on optimal energetic investment and future fitness returns is amenable to theoretical analyses, it can complicate empirical analyses, particularly in hermaphroditic species, in which energetic investment in male and female function, as well as fitness returns gained through each sex, are confounded within individuals. Although parental investment and optimality theories have provided many insights into how sex differences may have evolved, this approach can, unless applied with care, lead researchers to search for adaptations that “should” have been favored by selection.

THE OPPORTUNITY FOR SELECTION AND SEXUAL SELECTION

Estimates of the opportunity for selection, symbolized as I , measure the variance in relative fitness, V_w , and provide an empirical estimate of selection intensity. The value of I can be calculated for any population by dividing the variance in fitness, V_W , by the squared average fitness, W^2 . Fitness is easily and accurately measured as the number of offspring each individual produces. The ratio $V_W/W^2 = V_w$ describes the *opportunity* for selection because not all of the variation in parental fitness is heritable, and because by chance, an imperfect relationship exists between the actual variance in fitness, V_W , and the expected covariance between phenotype (z) and relative fitness ($w[z]$), $\text{Cov}(z, w[z])$.

Stated differently, bad things can happen to good phenotypes and vice versa, a point that addresses the possible effects of random processes on this measure of selection. The opportunity for selection places an upper boundary on the change in mean fitness itself, as well as on the standardized change in the mean value of all other phenotypic traits. In this way, it provides a dimensionless, empirical estimate of selection intensity that is useful for field and laboratory analysis.

Opportunity-for-selection theory identifies a sex difference in the variance in offspring numbers as the source of sexual selection. In contrast to parental investment theory, it identifies the magnitude of this fitness difference gained through male or female function as the ultimate cause of sex differences in energy allocated toward mating effort and parental care. The variance in offspring numbers is proportional to the strength of selection, and when some individuals mate and others do not, this variance in fitness can become large. If members of one sex have greater variance in offspring numbers than the other,

a sex difference in fitness will arise. Thus, the intensity of sexual selection is determined by the magnitude of the sex difference in the variance in offspring numbers.

MEASURING THE OPPORTUNITY FOR SEXUAL SELECTION

The source of a sex difference in the variance offspring numbers is easy to see, and it provides a simple, direct measure of the intensity of sexual selection. When the sex ratio equals 1 and all males and females mate once, there can be no sex difference in fitness variance. However, if certain individuals within each sex have more than one mate, other individuals within that sex must be excluded from mating, causing the variance in offspring numbers within that sex to increase. If the fraction of individuals excluded from mating is larger in one sex than it is in the other, a sex difference in the variance in offspring numbers will arise and be recognizable as the source of sexual selection. Estimates of OSR ($= N_\delta/N_\varphi = R_O = 1/R$) alone can provide misleading estimates of the actual intensity of sexual selection, because they say little about the *distribution* of matings per individual except in one special case; when all individuals mate *only once*.

Note that because each individual has a mother and a father, the average number of offspring, O , as well as the average number of mates, P , must be equal for each sex. Both expressions are linked through the sex ratio, thus $O_\varphi = R_O O_\delta$ and $P_\varphi = R_O P_\delta$. This necessary limitation is not considered in the “males-are-ardent, females-are-coy” dichotomy described in parental investment theory. If average fitness and average mate numbers must be equal for both sexes, neither sex can have greater average promiscuity than the other.

The total opportunity for selection for any species can be partitioned into separate selection opportunities for each sex. These components of total selection are equal to the variance in fitness among members of each sex, V_O (= the variance in offspring numbers across all individuals within that sex), divided by the squared average in fitness among members of that sex, O^2 (= the average number of offspring per individual, squared). For males, or when considering the intensity of selection on male function, $I_\delta = V_{O\delta}/O_\delta^2$. For females, or when considering the intensity of selection on female function, $I_\varphi = V_{O\varphi}/O_\varphi^2$.

The relationship between I_δ and I_φ is $I_\delta = R_O I_\varphi + I_{\text{mates}}$, where $R_O = N_\delta/N_\varphi$ and I_{mates} is the sex difference in the opportunity for selection that is due to differences in mate numbers among males. Note that both R_O and I_{mates} are part of this equation. When $R_O = 1$, subtracting I_φ from both sides of the above equation yields $I_\delta - I_\varphi =$

I_{mates} , demonstrating that the sex difference in the opportunity for selection, that is, the opportunity for *sexual selection*, is due to a difference in the variance in mate numbers, and thus in the variance in offspring numbers between the sexes.

SEXUAL SELECTION AND SEXUAL DIFFERENCES

Strong selection within one sex leads to sexual dimorphism because traits associated with high fitness are disproportionately transmitted to the next generation. For this reason, empirical estimates of the sex difference in the opportunity for selection predict whether and to what degree the sexes will diverge in character. For example, sexual selection in the intertidal isopod *Paracerceis sculpta* (Fig. 2A, B) can be 20 times stronger in males than in females. The sex difference in fitness variance is large because each female breeds only once, making the overall variance in female offspring numbers comparatively small. Breeding females prefer to aggregate within sponges, a condition that allows males who control these aggregations to mate many times. Polygyny by some males excludes other males from mating. This, in turn, makes the variance in male offspring numbers comparatively large.

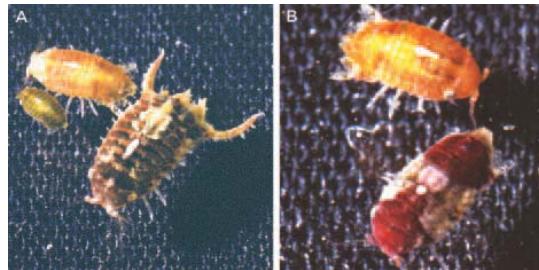


FIGURE 2 Three distinct male morphs coexist in the Gulf of California isopod *Paracerceis sculpta*: (A) α -males are largest, possess elongated uropods, and comprise 81% of aggregate male population samples; γ -males are smallest and comprise 15% of aggregate male population; β -males are smaller than α -males and comprise 4% of the male population; (B) β -males (above) also resemble females (below) in their behavior and external morphology; color patterns vary widely within and between individuals in this species. Photographs by the author.

The sex difference in fitness variance appears to be so large in this species that it allows three distinct male phenotypes to coexist. Although most males fight for aggregations, some males avoid combat altogether. They either mimic receptive females, or use their small size to enter sponges and mate. The three male morphs partition the available mates by exploiting different aspects of female

tendencies to enter sponges to breed. Strong sexual selection within each male type had favored particular morphologies that are distinct from females, and are distinct from one another.

The opportunity-for-selection approach predicts weak sexual selection in hermaphrodites if each individual reproduces proportionally as a male and as a female. However, if certain individuals emphasize male function when large or when crowded, variance in the number of offspring produced through male function can become large and sexual selection can become strong, as it appears to be in *Pseudoceros bifurcus* (Fig. 1). In these simultaneously hermaphroditic flatworms, some individuals may engage in more forced matings than other individuals. A sex difference in the opportunity for selection, in turn, is expected to favor differential allocation of energy toward mating or parental functions, as it does in other hermaphrodites such as sea slugs and leeches, and as it does in gonochorists, such as sea spiders, seahorses, and pipefish. Here, the intensity of selection favoring mate acquisition or parental care appears to shape observed patterns of sex allocation and parental investment, a causal chain that is the opposite of that predicted by parental investment theory.

HARMONIC MEAN PROMISCUITY AND SPERM COMPETITION

The opportunity for selection approach suggests that when multiple mating occurs, the fitness of an individual male depends on the number of ova he fertilizes, relative to the average number of ova fertilized by other males. In externally fertilizing species, multiple ejaculates are released simultaneously near ova and sperm mixing is common. Whereas sperm precedence is known in some internally fertilizing species, the advantage gained by the first or last male to mate with a female appears to erode steadily when the number of mating males becomes larger than 2.

Because of this relationship, a male's fertilization success in many species can be quantified as the reciprocal of the arithmetic mean of the reciprocals, of the promiscuity of each of his mates. Stated differently, a male's fertilization success, H_M , equals his mates' harmonic mean promiscuity, or,

$$1/H_M = 1/N_{\text{mates}} (\sum 1/P_i) \quad (\text{Eq. 1})$$

where N_{mates} equals the number of mates a male has, and P_i is the number of mates each i th female has, that

also mates with this male. For example, if a male mates with only one female and she mates only with him, the reciprocal of her "promiscuity" is $1/P = 1$. The arithmetic mean of this value is $(1/\text{mate})(1) = 1$, whose reciprocal is also 1. A male's fitness, then, equals the product of the harmonic mean promiscuity of his mates and the average number of offspring each female produces, or O_φ/H_M , where O_φ = the average number of offspring per female.

Now, if the male must abandon his current mate to mate with another female, and if his former mate mates again, $1/H_M = 1/2(1/2+1/1) = 0.75$, i.e., his fitness drops to $0.75O_\varphi$ per female. If the male extends his promiscuous search for mates, as parental investment and optimality theories predict he should, his fertilization success with past mates will continue to erode. Furthermore, if the females he encounters have already mated (i.e., their $P_i > 1$), a male's fitness loss with each additional mating will soon exceed his possible fitness gain. Because the harmonic mean is more strongly influenced by small numbers than by large numbers, this approach shows why selection is likely to favor male tendencies to reduce, rather than enhance, their own promiscuity as well as that of their mates, a result supported by the ubiquity of mate guarding among gonochorists, as well as by prolonged mating associations and reduced sperm production in hermaphrodites.

The foregoing approach illustrates another principle often unrecognized in discussions of sperm competition from parental investment or optimality perspectives. While sperm numbers within multiply mated females may change the distribution of male paternity *within* broods, it need not affect the distribution of paternity *among* broods. Thus, sperm competition represents a significant evolutionary force *only* when males who mate with disproportionate success *also* have sperm that are disproportionately used to fertilize ova by each of the females with whom they mate.

If this relationship does not exist (and often it does not), multiple mating or other mechanisms that reduce paternity confidence (e.g., sperm digestion) will ameliorate rather than intensify sexual selection. This prediction is at odds with optimal expectations for increased energy allocation toward male function when multiple mating occurs. Using genetic markers to document offspring numbers, empirical values of H_M and of the sex difference in the opportunity for selection, I_{mates} , provide a means for assessing the source, as well as the actual intensity, of sexual selection on observed patterns of parental investment and sex allocation.

A FOCUS ON EVOLUTIONARY PROCESS

In contrast to parental investment and sex allocation theories, opportunity-for-selection theory focuses on *evolutionary processes*. By specifically measuring the fitness variance associated with patterns of sex allocation and parental care, this approach identifies traits on which selection may be strong or weak. Furthermore, this approach complements research on the genetic basis of sex allocation and parental care, which to date is largely unstudied, particularly among species inhabiting rocky intertidal zones. Because phenotypic change depends on the product of selection intensity and trait heritability, investigations that measure fitness variance as well as patterns of trait inheritance can identify which phenotypes are likely to respond to selection and by how much. This evolutionary genetic approach generates hypotheses about selection and inheritance that are specifically falsifiable using the data generated by analyses of fitness variance and trait expression.

By focusing on evolutionary processes rather than on presumed adaptive outcomes, opportunity-for-selection theory provides an experimental framework for investigating phenomena that are specifically avoided by parental investment and optimality approaches. In many cases, hypotheses focused on evolutionary processes are simpler, more rigorously testable, and easier to interpret than hypotheses focused on evolutionary outcome. Few studies have measured evolutionary processes in rocky intertidal habitats. There is much exciting work to be done.

SEE ALSO THE FOLLOWING ARTICLES

Fertilization, Mechanics of / Genetic Variation and Population Structure / Reproduction

FURTHER READING

- Ahnesjö, I., C. Kvarnemo, and S. Merilaita. 2001. Using potential reproductive rates to predict mating competition among individuals qualified to mate. *Behavioral Ecology* 12: 397–401.
- Alcock, J. 2005. *Animal behavior: an evolutionary approach*. 8th ed. Sunderland, MA: Sinauer Associates.
- Charnov, E. L. 1996. Sperm competition and sex allocation in simultaneous hermaphrodites. *Evolutionary Ecology* 10: 457–462.
- Cheverud, J. M., and A. J. Moore. 1994. Quantitative genetics and the role of the environment provided by relatives in the evolution of behavior, in *Quantitative genetic studies of behavioral evolution*. C. R. B. Boake, ed. Chicago: University of Chicago Press, 67–100.
- Frank, S. A. 1990. Sex allocation theory for birds and mammals. *Annual Review of Ecology and Systematics* 21: 13–55.
- Schärer, L., P. Sandner, and N. K. Michiels. 2005. Trade-off between male and female allocation in the simultaneously hermaphroditic flatworm *Macrostomum* sp. J. *Evolutionary Biology* 18: 396–404.

- Shuster, S. M., and M. J. Wade. 2003. *Mating systems and strategies*. Princeton, NJ: Princeton University Press.
- Wade, M. J. 1979. Sexual selection and variance in reproductive success. *The American Naturalist* 114: 742–764.

SHRIMPS

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Shrimps found on rocky intertidal shores are usually members of the infraorder Caridea (Crustacea: Decapoda). Carideans typically have two (never three) pairs of pincer-like appendages (chelipeds), the second pleura (side plates) of the tail (abdomen) overlaps adjacent pleura, and females brood their embryos below the abdomen. Shrimps can withstand little or no exposure at low tide and are thus restricted in the rocky intertidal zone to water-filled pools and channels. Carideans may be abundant in the rocky intertidal habitat and are ecologically important in trophic webs as small predators, herbivores, and detritivores as well as serving as prey of larger organisms such as fishes.

MORPHOLOGY AND TAXONOMY

The body of a shrimp (Fig. 1) is divided into an anterior cephalothorax and a posterior abdomen (tail). The first antennae bear the olfactory hairs (setae), while the second antennae have long, flexible flagella with taste and touch receptors. The three primary pairs of mouthparts



FIGURE 1 *Heptacarpus sitchensis*, a typical hippolytid caridean shrimp (a color morph with a green abdomen and striped cephalothorax). Photograph by the author.