SEX-RATIO BIAS AND CLONAL REPRODUCTION IN THE BRITTLE STAR *OPHIACTIS SAVIGNYI*

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Abstract.—Although the sex ratios of many groups conform to Fisher's (1930) prediction that parents should invest equally in daughters and sons, a number of taxa are characterized by excesses of one gender. A variety of mechanisms may lead to sex ratio biases, but in organisms that reproduce clonally as well as sexually, gender differences in the rate of cloning could drive the development of sex-ratio biases. In this study, I demonstrate that males of the clonal brittle star *Ophiactis savignyi* were significantly more likely to divide than females and that the magnitude of this difference was sufficient to explain the consistent and significant excess of males in natural populations. Females were significantly more likely to lose sexual reproductive capabilities following division, and this greater cost associated with division may explain why females are less likely to divide. Gender differences in mortality rates are unlikely to explain the excess of males in this species. Because of their potential influence on the operational sex ratio, gender differences in division rates may have important ecological and evolutionary implications including effects on the direction and strength of selection.

Key words.—Brittle star, clonal reproduction, costs, gender-specific strategies, sex-ratio bias.

The sex ratios of natural populations have been of interest to biologists at least since Darwin (1871). Fisher (1930) proposed a simple and elegant frequency-dependent model predicting equal investment in daughters and sons. This prediction is upheld in many organisms, but deviations from even sex ratios occur and may even be the norm in a number of taxa (reviewed in Meagher 1981; Charnov 1982; Bull and Charnov 1988; Antolin 1993). Because the sex ratio can determine the strength and direction of selection on traits related to mating (e.g., Emlen and Oring 1977), the study of sex ratios and how sex ratios become biased have been extremely active areas of inquiry in biology.

Under some conditions, selection may favor the overproduction of offspring of one gender (reviewed in Frank 1990; Antolin 1993), creating a bias in the primary sex ratio (i.e., the sex ratio at birth). Sex-ratio biases may also develop secondarily from an initially even primary ratio if females and males differ in various aspects of their life histories (Lloyd and Webb 1977; Allen and Antos 1993; McLetchie and Puterbaugh 2000). Numerous authors have suggested that differences between the genders in rates of mortality could be responsible for sex-ratio biases (Lloyd 1973; Lovett Doust and Lovett Doust 1988; Allen and Antos 1993; Uthicke et al. 1999). Biases in the operational sex ratio (i.e., the sex ratio of individuals in breeding condition) may also arise if females and males differ in the age or size at which they reach maturity (Bawa et al. 1982; Lovett Doust and Laporte 1991; Garcia and Antor 1995) or the frequency with which they reproduce (Bawa et al. 1982; Levitan 1988; Lovett Doust and Lovett Doust 1988; Houssard et al. 1994; Garcia and Antor 1995).

In organisms that reproduce clonally (asexually), sex-ratio biases may also arise if females and males differ in the rates at which they produce clonemates, a possibility suggested by numerous authors (Darwin 1877; Lloyd and Webb 1977; Sa-

kai and Burris 1985). Despite the long history of interest in the potential impact of cloning on sex ratios, however, only a few studies on clonal plants have demonstrated gender differences in rates of clonal reproduction (e.g., Putwain and Harper 1972; Popp and Reinartz 1988; Houssard et al. 1994; Williams 1995). There is a similar paucity of studies examining this mechanism in animal taxa. Although patterns of clonal structure in several animal species could potentially be construed as evidence for gender differences in cloning (e.g., Uthicke et al. 1999), these studies fail to explicitly examine the division rates of individuals and frequently attribute sex-ratio biases to the action of some other mechanism.

The genders may differ in their rates of cloning if they differ in the costs associated with cloning. Although the costs associated with cloning may take various forms, costs to the sexual production of offspring are of great importance for both genetic and ecological reasons. Sexual reproduction may facilitate adaptation to changing conditions (Peck 1994; Holsinger 2000) by allowing the elimination of deleterious mutations (Kondrashov 1988; Holsinger 2000) and the spread of beneficial ones (reviewed in Hurst and Peck 1996). The novel gene combinations produced during recombination may enhance the abilities of an individual's progeny to exploit spatial or temporal variation in habitats (reviewed in Hurst and Peck 1996). Because of its connection with dispersal in many organisms (Abrahamson 1975; Williams 1975; Highsmith 1982; Sebens and Thorne 1985), sexual reproduction may also allow progeny to be transported away from a habitat that is degraded or in the process of degrading (Williams 1975) or a habitat in which an individual is likely to compete with siblings or parents. Therefore, sexual offspring may be the best way to insure continued genetic representation of a clone, and the effects of cloning on sexual reproductive capabilities should be of great importance in the evolution of clonal strategies.

Cloning may benefit the long-term sexual capabilities of the clone as a whole. The existence of multiple clonemates

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may increase the number of bodies that can produce gametes (Highsmith 1982; Hughes and Cancino 1985; Mladenov and Emson 1990) as well as the spatial distribution of the clone, making it more likely that clonemates are near potential mates (Handel 1985; Lasker et al. 1996; McLetchie and Puterbaugh 2000). Increasing the number of clonemates should also decrease the risk of whole-clone mortality, assuming some independence of mortality between clonemates (Cook 1979; Highsmith 1982; Hughes and Cancino 1985; Hughes et al. 1992). This risk-spreading should increase the longevity of the clone (Watkinson and White 1985; Schmid 1990) and the number of reproductive seasons the clone experiences.

Costs to sexual capabilities associated with cloning may arise due to the diversion of resources away from the production of gametes (Emson and Wilkie 1980; Gasser et al. 2000) or by the division of a single large individual into several small individuals that are less likely to be mature (Hughes and Jackson 1985; Karlson 1986; Smith and Hughes 1999). Gender differences in these costs may result in selection for differences in the rates at which females and males produce new clonemates. Gender differences in the rate of cloning could result in the accumulation of individuals of one gender and therefore a sex-ratio bias in the population.

Past observers (Mladenov and Emson 1988; Chao and Tsai 1995) have reported male-biased sex ratios in populations of the clonal brittle star *Ophiactis savignyi*. In this study, I document the extent to which populations of this species are male biased in the Florida Keys. I then experimentally assess the potential role of gender differences in clonal reproduction in the generation of this bias. I present evidence on gender-specific costs to sexual capabilities associated with cloning and relate these differences to gender-specific patterns of clonal division. Additionally, I address whether gender differences in various other aspects of their life histories, specifically mortality rates and the sexual reproductive size thresholds reported in McGovern (2002), could contribute to the bias.

MATERIALS AND METHODS

Study Organism

The brittle star *O. savignyi* (Echinodermata, Ophiuroidea) is a small-bodied species (0.5–11 mm disc diameter; McGovern 2002) that ranges throughout the world in the tropics (Mladenov and Emson 1990; Chao and Tsai 1995). *Ophiactis savignyi* frequently lives in association with marine sponges, where it may be found in very high densities (Mladenov and Emson 1990; Chao and Tsai 1995; McGovern 2002). *Ophiactis savignyi* is dioecious and reproduces sexually by broadcasting gametes into the water. At any given time, only a relatively small proportion of individuals is sexually mature (1.5–16.1%), and the peak sexual activity is late summer through fall (McGovern 2002). Following the sexual reproductive peak, animals typically decrease in size and no longer have gonads (T. M. McGovern, unpubl. data). Sexual reproduction is size rather than age based, and females and males differ in their sexual reproductive size thresholds: Females must be slightly but significantly larger than males before they contain gonads (4.6 mm and 5.2 mm disc diameter, average size of mature females and males, respectively; Mc-

Govern 2002). Individuals of this species also reproduce asexually by splitting across their discs (disc fission) and each half then regenerates the missing portion of the disc and the three lost arms (Emson and Wilkie 1980). Low clonal diversity within any sponge population (Mladenov and Emson 1990) suggests that recruitment into a population occurs primarily through clonal rather than sexual reproduction.

Sex Ratios in Natural Populations of Ophiactis savignyi

I sampled *O. savignyi* approximately every 4–8 weeks from March 1996 through October 1998 from areas around Long Key, Florida. In each sampling period, I hand-collected sponges, finely dissected each, and removed all brittle stars residing within the sponge (hereafter termed a ''population''). Once removed from the sponge host, each population of brittle stars was maintained in running seawater and was isolated from other populations. Each population was sampled only once, and was therefore considered to be independent from all other populations in the examination of the sex ratio across sampling periods.

Following removal from the sponge hosts, each brittle star from each population was anesthetized in magnesium chloride (Mladenov et al. 1983). I determined the sex of each individual by inspection of the gonads (when present) through the skin of animals with large well-developed gonads and by minor dissection into the bursal cavities of animals with smaller gonads. Testes and ovaries were easily distinguished on the basis of color and structure (McGovern 2002). I calculated the sex ratio (proportion male) for each population in which at least a single mature animal was found and the average sex ratio across populations within each sampling period. For each sampling period, I calculated the 95% confidence interval around the mean sex ratio using the formula: mean $\pm 1.96(SD/n^{0.5})$, where n is the sample size (Sokal and Rohlf 1987). Significant deviations from an even sex ratio were indicated when the 95% confidence interval within any sampling period did not include the even sex ratio (0.5). I also calculated the overall sex ratio across all sampling periods to determine if the even sex ratio fell within the 95% confidence interval around that estimate.

Experimental Observations

Probability of division

To determine if females and males differed in their probability of division, I followed individuals of known gender through time in a field experiment. Animals were collected, anaesthetized, and sexed in October 1998. I also measured the disc diameter of each individual at the widest point, a measure that is highly correlated with body mass (McGovern 2002). Each mature animal was marked with an identifying sequence of spots using the vital dyes methylene blue and congo red. In prior tests, I had determined that these marks would remain on animals of mature size (~3–4 mm disc diameter or greater; McGovern 2002) in field conditions for 6 weeks or more. Marked individuals were then introduced into containers constructed from cut-up pieces of plastic tubing wrapped in a large-mesh fabric. The tubing provided crevices in which the animals could hide and the wide mesh

gave the animals access to water-borne food particles. Following introduction of the animals, the containers were suspended approximately 30 cm above the substrate from PVC and monofilament frames. These frames were situated approximately 35 m offshore from the Keys Marine Lab on Long Key, Florida, at a depth of 1.5 m. The experimental site was not different in any obvious characteristics from locations where I typically collected *O. savignyi*. In prior experiments, recovery rates of animals from the experimental containers from the same site were generally high (mean recovery = 74%, SD = 17%). Because it is impossible to follow individuals through time without caging them, it was not possible to determine whether the experimental containers themselves affected absolute levels of division or disappearance (see below). Because arguments pertaining to the development of a biased sex ratio depend on relative rates of division, and possibly mortality, of female and male individuals, however, caging effects should not present a problem in interpretation as long as they are experienced equally by both sexes. There is no reason to suspect that the containers would affect females and males differently.

Animals were placed into four treatment groups: single females, single males, paired females, and paired males. The single-sex pairs were initiated as a control for density in a parallel experiment examining the effect of a potential mate on rates of division (McGovern 2001). Each treatment group was replicated eight times, and I made every attempt to match animals by size within each set of the four treatments. The experiment was begun in October 1998. In every month from November 1998 through June 1999, I removed animals from their containers and determined which animals were still present and which had divided. In addition, I measured the disc diameter and determined the sexual status of each individual and reapplied each individual's mark. At the end of the experiment, I calculated the probability of division in each replicate by dividing the number of observed divisions by the number of possible divisions. I calculated the number of possible divisions by counting the number of instances in which I could determine whether an individual animal had divided between sampling events. This required that the individual (or its descendent halves) was present in consecutive censuses. Clonemates produced during the course of the experiment were counted as separate individuals with independent chances for division in the months following their separation. This metric (actual/possible divisions) controlled for instances in which animals divided repeatedly or disappeared before the end of the experiment. For treatments in which two animals were present (the same-sex pairs), the probability of division was averaged across individuals, weighted by the number of possible divisions for each.

Before examining the effect of gender on the probability of division, I first determined if there was any effect of density within each sex by comparing treatments with one and two individuals using Mann-Whitney *U*-tests. If it was determined that density did not affect the probability of division, I pooled these treatments within gender. Data could not be transformed to meet the assumptions of normality due the presence of many zero values, particularly among females (representing animals that never divided), so the comparison of the division probabilities of females and males was made using a Mann-Whitney *U*-test.

Gender-dependent costs of cloning

Because I measured body size and examined every animal for the presence of gonads in each month of the field experiment, I could monitor the change in size and sexual status of any dividing animals. Division of mature females was rare (see below); therefore, I pooled data from the experiment described above and an earlier experiment to examine the effect of gender on both these responses. Data from the earlier experiment were used only to examine costs of clonal division, and not division rates, because the conditions and time of year in which the experiment was conducted differed from those described above.

Decrease in body size following division was calculated as the average size of the two halves (when both were present) subtracted from the predivision size. If only a single half remained, that individual's size was subtracted from the predivision size. The size decreases of females and males were compared using a *t*-test. The change in sexual status of animals following division was used to estimate the potential cost of cloning to sexual reproductive capabilities. Mature animals have a pair of gonads associated with each arm, so, in theory, both halves produced when a mature animal divides could still be sexually mature. Alternatively, one or both halves may lose their gonads, presumably by resorbing them. Resorption of gonads has been noted in other echinoderm species during periods of stress (Lawrence 1987; Levitan 1991 and references therein). Due to the low numbers of mature females that divided, I combined these categories (loss of gonads in one or both halves) to represent a cost of division. Determining reproductive costs of division by assaying for the presence of gonads may underestimate the loss of reproductive potential to some degree. Per-gonad mass is known to decrease in recently divided animals (T. M. McGovern, unpubl. ms.), so divisions that were termed ''no cost'' in this study may in fact have had decreased gamete-producing capabilities. Females and males do not differ in the relationship between per-gonad mass and the recency of division, however, and measuring cost as the absence of gonads provided a quick, nondestructive assay for cost to sexual capabilities. I determined whether females and males differed in the cost associated with division using a chi-squared test.

Disappearance rates

In addition to the potential effect of differences in division, differences in mortality could also affect the sex ratio. As a surrogate for mortality, I measured the rates of disappearance of female and male animals from single-sex treatments of the field experiment described above. Although it is not currently possible to unambiguously assign these disappearances to either mortality or migration, the magnitude and direction of any bias in disappearance rates could at least suggest whether mortality might be important in the generation of the sex-ratio bias. A disappearance was recorded whenever an individual was no longer present in the experimental container. The disappearance rates of animals of known gender ($n = 16$ for both genders) were calculated by dividing the number

TABLE 1. Sex ratios in 20 sampling periods over 31 months. *N* is the number of populations in each period with mature individuals, sex ratio is the proportion male, and SD is the standard deviation of the sex ratio estimate. Male-biased sex ratios are in bold, and significant departures from an even sex ratio (0.50) are indicated with an asterisk.

Sampling period	*N*	Sex ratio	SD
March 1996	8	**0.67**	0.47
May 1996	7	**0.81***	0.38
July 1996	7	0.40	0.43
August 1996	9	**0.77***	0.34
September 1996	6	**0.77**	0.41
October 1996	9	**0.65**	0.41
December 1996	4	**0.58**	0.50
February 1997	4	**0.75**	0.50
March 1997	3	**0.67**	0.58
June 1997	7	**0.86***	0.38
July 1997	3	**0.72**	0.25
August 1997	10	**0.58**	0.50
October 1997	7	**0.85***	0.27
November 1997	11	**0.56**	0.38
January 1998	7	0.39	0.46
March 1998	10	**0.76**	0.42
May 1998	6	**0.71**	0.40
June 1998	7	**0.68**	0.47
August 1998	6	0.35	0.44
October 1998	5	0.37	0.44

FIG. 1. Cost associated with clonal division (loss of gonads in one or both halves) for females and males.

of actual disappearances in each replicate by the number of possible disappearances. This allowed the disappearances of clonemates produced during the course of the experiment to be considered as separate events. The effect of gender on the proportion of animals that disappeared during the experiment was examined using a *t*-test on fourth-root-transformed data.

RESULTS

Sex Ratios in Natural Populations of Ophiactis savignyi

The sex ratio was male biased in 16 of the 20 sampling periods (Table 1), and the male bias was significant in four of these periods. In the four sampling periods in which a female bias was detected, the bias was never significant, and the deviation from an even sex ratio in the female-biased months (the absolute value of the sex ratio − 0.5) was lower than the deviation observed in male-biased periods (average deviation = 0.127 and 0.214 for female- and male-biased periods, respectively). This difference was only marginally significant ($t = 1.94$, $P = 0.068$), but suggests that female biases were less extreme, on average, than male biases. When the sex ratio was calculated over all populations across sampling periods, the average sex ratio was 0.65 and the 95% confidence interval for this estimate was 0.58–0.72.

Experimental Observations

Probability of division

Density (the effect of being alone vs. having a member of the same sex present) did not affect the probability of division in either sex (females: $U = 30$, $P > 0.2$; males: $U = 33.5$, $P > 0.2$), so density treatments were pooled within gender. Males were nearly 3.5 times more likely to divide than females throughout the course of the experiment, and this effect was significant ($U = 179$, $P = 0.02$). Of the 24 animals of
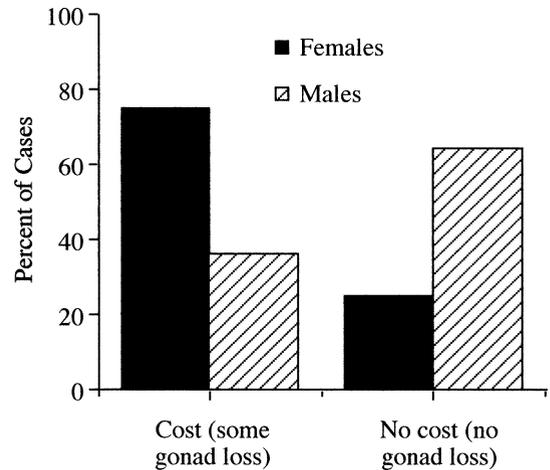
each sex used to initiate the treatments, 16 females never divided, whereas only eight males failed to divide during the course of the experiment.

Gender-dependent costs of cloning

There was no difference in the degree to which females and males decreased in size following division ($t = 0.27$, $P = 0.788$): Disc diameters decreased by 1.25 mm (27%) in females ($n = 12$) and by 1.21 mm (25%) in males ($n = 28$). Females and males did differ in the costs to sexual reproductive capabilities associated with clonal reproduction, however. Most divisions of mature females (8 of 12, 75%) resulted in the loss of gonads in one or both halves. When mature males divided, however, most cases (18 of 28, 64%) resulted in no such loss (Fig. 1). This difference between the genders in the cost associated with division was marginally significant ($\chi^2 = 3.28$, $P = 0.070$).

Disappearance rates

Disappearance rates of both genders were low in the first two months of the experiment. Beginning in January 1999, however, disappearance of animals, particularly males, increased (Fig. 2). The proportion of males disappearing remained high and was two or more times higher than the disappearance rate of females in many of the following months. The disappearance rate of males declined at the end of the experiment because there were only two remaining individuals in May, both of which were still present in June. By the end of the experiment in June 1999, 13 females remained in the experiment, whereas there were only two remaining males, despite the fact that there were 24 animals of each gender at the onset of the experiment and males were more than 3.5 times more likely to produce clonemates during the course of the experiment. The average proportion of males disappearing from the experiment by the end of the experiment was significantly greater than the proportion of females disappearing ($t = 2.68$, $P = 0.012$). There was no immigration into the experimental containers.
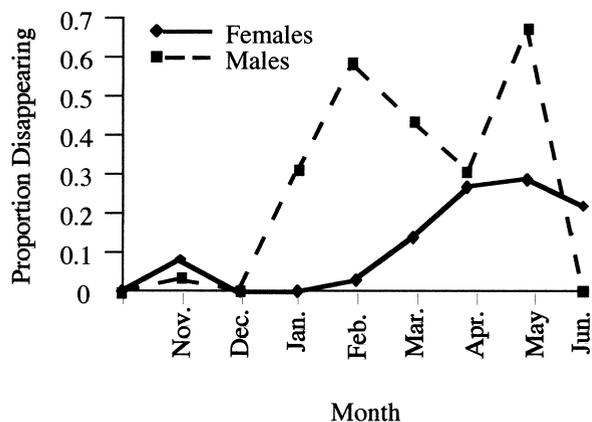
FIG. 2. Proportion of animals disappearing in each month from single-sex female and male treatments.

DISCUSSION

Populations of the clonal brittle star *O. savignyi* were consistently male biased in 20 sampling periods over the course of 31 months; in four periods, the bias toward males was significant. In the four periods in which the average sex ratio was less than 50% males, the deviations from an even sex ratio were not significant, and female biases were generally less extreme than male biases. The average sex ratio across the entire sampling period (0.65) was significantly greater than the even sex ratio predicted by Fisher (1930).

Gender differences in clonal reproductive rates may explain the sex-ratio bias in *O. savignyi*. Males were nearly 3.5 times more likely than females to divide over the course of the field experiment, a difference more than sufficient to explain the male bias in the sex ratio. Most males (67%) divided at least once during the course of the experiment, whereas only 33% of females divided throughout the same period. Whereas gender differences in cloning could clearly contribute to the preponderance of females in species in which only a single gender clones (as occurs in parthenogenetic organisms; e.g., Samadi et al. 1999), far fewer studies (Putwain and Harper 1972; Popp and Reinartz 1988; Houssard et al. 1994; Williams 1995) have examined the contribution of clonal reproduction to sex-ratio biases in species in which both genders clone. The paucity of such studies comes despite the long-recognized potential for clonal reproduction to contribute to sex-ratio biases (Darwin 1877; Lloyd and Webb 1977; Sakai and Burris 1985).

In addition to providing evidence for differences in division probabilities, this study also points to a potential explanation for why the genders differ in their rates of cloning. Clonal division was less costly to the sexual capabilities of male animals: Most males retained testes in both halves following division. In the majority of cases in which a mature female divided, however, there was a loss of ovaries in one or both halves, indicating that females were less able to simultaneously engage in sexual and clonal reproduction. The necessity of regenerating half of the body following division is likely to exert a strong demand for resources, as suggested by the decrease in size of dividing individuals and the loss of gonads in some post-division animals. The differences

between the genders in the reproductive cost associated with cloning may result from a combination of the size decrease associated with reproduction and differences in the reproductive size thresholds of females and males (McGovern 2002). Decreases in size and the resorption of gonads have been noted in other echinoderm species when animals become energy limited (e.g., during starvation, Lawrence 1987; Levitan 1991 and references therein).

Besides the potential influence of differences in division rates, other life-history differences between females and males may also contribute to the sex-ratio bias in *O. savignyi*. In addition to their possible role in the different costs associated with cloning, differences in the sexual reproductive size thresholds of female and male *O. savignyi* (McGovern 2002) may contribute directly to the observed sex-ratio biases in this species. Because males can reproduce sexually at smaller sizes, it is expected that a greater proportion of male individuals would attain sexual maturity, which would lead to a male-biased operational sex ratio. A role for differences in the size threshold of sexual maturity in the generation of male-biased operational sex ratios has also been implicated in a number of plant species in which females were less likely to be mature (Bawa et al. 1982; Lovett Doust and Laporte 1991; Garcia and Antor 1995).

Differences between the genders in mortality rates have also been cited as an explanation for biased sex ratios in a number of species, clonal and otherwise (see introduction). It is unlikely that gender differences in mortality account for the male bias in *O. savignyi*, however. Male individuals had dramatically greater rates of disappearance from the field experiment than females in all months beginning in January 1999. Although it is not currently possible to unambiguously assign these disappearances to mortality, the gender bias in disappearance rates is in the opposite direction to that which would explain the male-biased sex ratios observed in this species, and if anything, would mitigate the effects of differential clonal proliferation on sex ratios in *O. savignyi*.

Although sex-ratio biases may arise in clonal species in several ways, the differences in division rates of female and male *O. savignyi* are of a magnitude and direction sufficient to explain the excess of males in natural populations. This bias in the operational sex ratio may have important ecological and evolutionary consequences if it creates asymmetries in the levels of intrasexual competition. For example, Perrin and Mazalov (2000) predict that the gender that experiences the greatest degree of intrasexual competition with relatives should be more likely to disperse. Asymmetries in intrasexual competition may also alter the strength or even the direction of sexual selection (Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996; Levitan 1998; Ashman and Diefenderfer 2001).

In *O. savignyi*, the biased operational sex ratio could lead to selection on traits related to reproduction by altering the conditions under which gametes interact. In most broadcast spawners, mating systems can typically be characterized as sperm limited (reviewed in Levitan 1998). An operational sex ratio biased toward males may transform this sperm-limited condition to one in which sperm compete to fertilize eggs. Under conditions of sperm competition, the variance in reproductive success is expected to be asymmetrical (with

females having lower variance), setting the stage for divergent evolution in both morphology and behavior (Emlen and Oring 1977; Levitan 1998). The extent to which gender differences in rates of cloning may alter selective pressures on behavior or mating systems has received little attention, particularly in animals, but should provide ample fodder for future theoretical and empirical investigations given the prevalence of clonal reproduction in both animal and plant taxa.

LITERATURE CITED

Abrahamson, W. G. 1975. Reproductive strategies in dewberries. Ecology 56:721–726.
Allen, G. A., and J. A. Antos. 1993. Sex ratio variation in the dioecious shrub *Oemleria cerasiformis*. Am. Nat. 141:527–553.
Antolin, M. F. 1993. Genetics of biased sex ratios in subdivided populations: models, assumptions, and evidence. Oxf. Surv. Evol. Biol. 9:239–281.
Ashman, T. L., and C. Diefenderfer. 2001. Sex ratio represents a unique context for sexual selection on attractive traits: consequences for the evolution of sexual dimorphism. Am. Nat. 157:334–347.
Bawa, K. S., C. R. Keegan, and R. H. Voss. 1982. Sexual dimorphism in *Aralia nudicaulis* L. (Araliaceae). Evolution 36:371–378.
Bull, J. J., and E. L. Charnov. 1988. How fundamental are Fisherian sex ratios? Oxf. Surv. Evol. Biol. 5:96–135.
Chao, S. M., and C. C. Tsai. 1995. Reproduction and population dynamics of the fissiparous brittle star *Ophiactis savignyi* (Echinodermata: Ophiuroidea). Mar. Biol. 124:77–83.
Charnov, E. L. 1982. The theory of sex allocation. Princeton Univ. Press, Princeton, NJ.
Cook, R. E. 1979. Asexual reproduction: a further consideration. Am. Nat. 113:769–772.
Darwin, C. 1871. The descent of man, and selection in relation to sex. J. Murray, London.
———. 1877. The different forms of flowers on plants of the same species. J. Murray, London.
Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215–223.
Emson, R. H., and I. C. Wilke. 1980. Fission and autotomy in Echinoderms. Oceanog. Mar. Biol. Annu. Rev. 18:155–250.
Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon, Oxford, U.K.
Frank, S. A. 1990. Sex allocation theory for birds and mammals. Annu. Rev. Ecol. Syst. 21:13–55.
Garcia, M. B., and R. J. Antor. 1995. Sex ratio and sexual dimorphism in the dioecious *Borderea pyrenaica*. Oecologia 101:59–67.
Gasser, M., M. Kaiser, D. Berrigan, and S. C. Stearns. 2000. Life history correlates of evolution under high and low adult mortality. Evolution 54:1260–1272.
Handel, S. N. 1985. The intrusion of clonal growth patterns on plant breeding systems. Am. Nat. 125:367–384.
Highsmith, R. C. 1982. Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7:207–226.

Holsinger, K. E. 2000. Reproductive systems and evolution in vascular plants. Proc. Natl. Acad. Sci. 97:7037–7042.
Houssard, C., J. D. Thompson, and J. Escarré. 1994. Do sex-related differences in response to environmental variation influence the sex ratio in the dioecious *Rumex acetosella*? Oikos 70:80–90.
Hughes, R. N., and J. M. Cancino. 1985. An ecological overview of cloning in Metazoan. Pp. 153–186 in J. B. C. Jackson, L. W. Buss, and R. E. Cook, eds. Population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT.
Hughes, T. P., and J. B. C. Jackson. 1985. Population dynamics and life histories of foliaceous corals. Ecol. Monogr. 55:141–166.
Hughes, T. P., D. J. Ayre, and J. H. Connell. 1992. The evolutionary ecology of corals. Trends Ecol. Evol. 7:292–295.
Hurst, L. D., and J. R. Peck. 1996. Recent advances in understanding of the evolution and maintenance of sex. Trends Ecol. Evol. 11:46–52.
Karlson, R. H. 1986. Disturbance, colonial fragmentation, and size-dependent life history variation in two coral reef cnidarians. Mar. Ecol. Prog. Ser. 28:245–249.
Kondrashov, A. 1988. Deleterious mutations and the evolution of sexual reproduction. Nature 336:435–440.
Kvarnemo, C., and I. Ahnesjö. 1996. The dynamics of operational sex ratios and competition for mates. Trends Ecol. Evol. 11:404–408.
Lasker, H. R., D. A. Brazeau, J. Calderon, M. A. Coffroth, R. Coma, and K. Kim. 1996. *In situ* rates of fertilization among broadcast spawning gorgonian corals. Biol. Bull. 190:45–55.
Lawrence, J. 1987. A functional biology of echinoderms. Johns Hopkins Univ. Press, Baltimore, MD.
Levitan, D. R. 1988. Asynchronous spawning and aggregative behavior in the sea urchin *Diadema antillarum* Philippi. Pp. 181–186 in R. Burke R, ed. Proceedings of the sixth international echinoderm conference, Victoria, BC. Balkema Press, Rotterdam.
———. 1991. Skeletal changes in the test and jaw of the sea urchin *Diadema antillarum* in response to food limitation. Mar. Biol. 111:421–435.
———. 1998. Sperm limitation, gamete competition, and sexual selection in external fertilizers. Pp. 175–217 in T. R. Birkhead and A. P. Møller, eds. Sperm competition and sexual selection. Academic Press, San Diego, CA.
Lloyd, D. G. 1973. Sex ratios in sexually dimorphic Umbelliferae. Heredity 31:239–249.
Lloyd, D. G., and C. J. Webb. 1977. Secondary sex characters in plants. Bot. Rev. 43:177–216.
Lovett Doust, J., and G. Laporte. 1991. Population sex ratios, population mixtures and fecundity in a clonal dioecious macrophyte, *Vallisneria americana*. J. Ecol. 79:477–489.
Lovett Doust, J., and L. Lovett Doust. 1988. Modules of production and reproduction in a dioecious clonal shrub, *Rhus typhina*. Ecology 69:741–750.
McGovern, T. M. 2001. Clonal reproduction and sex ratio bias in the brittle star *Ophiactis savignyi*. Ph.D. diss., Florida State University, Tallahassee, FL.
———. 2002. Patterns of sexual and asexual reproduction in the brittle star *Ophiactis savignyi* (Echinodermata, Ophiuroidea) in the Florida Keys. Mar. Ecol. Prog. Ser., In press.
McLetchie, D. N., and M. N. Puterbaugh. 2000. Population sex ratios, sex-specific clonal traits and trade-offs among these traits in the liverwort *Marchantia inflexa*. Oikos 90:227–237.
Meagher, T. R. 1981. Population biology of *Chamaelirium luteum*, a dioecious lily. II. Mechanisms governing sex ratios. Evolution 35:557–567.
Mladenov, P. V., and R. H. Emson. 1988. Density, size structure and reproductive characteristics of fissiparous brittle stars in algae and sponges: evidence for interpopulational variation in levels of sexual and asexual reproduction. Mar. Ecol. Prog. Ser. 42:181–194.
———. 1990. Genetic structure of populations of two closely related brittle stars with contrasting sexual and asexual life histories, with observations on the genetic structure of a second asexual species. Mar. Biol. 104:265–274.

Mladenov, P. V., R. H. Emson, L. V. Colpit, and I. C. Wilkie. 1983. Asexual reproduction in the West Indian brittle star *Ophicomella ophiactoides* (H. L. Clark) (Echinodermata: Ophiuroidea). J. Exp. Mar. Biol. Ecol. 72:1–23.

Peck, J. R. 1994. A ruby in the rubbish: beneficial mutations, deleterious mutation and the evolution of sex. Genetics 137: 597–606.

Perrin, N., and V. Mazalov. 2000. Local competition, inbreeding and the evolution of sex-biased dispersal. Am. Nat. 155: 116–127.

Popp, J. W., and J. A. Reinartz. 1988. Sexual dimorphism in biomass allocation and clonal growth of *Xanthoxylum americanum*. Am. J. Bot. 75:1732–1741.

Putwain, P. D., and J. L. Harper. 1972. Studies in the dynamics of plant populations. J. Ecol. 60:113–129.

Sakai, A. K., and T. A. Burris. 1985. Growth in male and female aspen clones: a twenty-five year longitudinal study. Ecology 66: 1921–1927.

Samadi, S., J. Mavarez, J. P. Pointier, B. Delay, and P. Jarne. 1999. Microsatellite and morphological analysis of population structure in the parthenogenetic freshwater snail *Melanoides tuberculata*: insights into the creation of clonal variability. Mol. Ecol. 8:1141–1153.

Schmid, B. 1990. Some ecological and evolutionary consequences of modular organization and clonal growth in plants. Evol. Trends Plants 4:25–34.

Sebens, K. P., and B. L. Thorne. 1985. Coexistence of clones, clonal diversity, and the effects of disturbance. Pp. 357–398 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, eds. Population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT.

Smith, L. D., and T. P. Hughes. 1999. An experimental assessment of survival, re-attachment and fecundity of coral fragments. J. Exp. Mar. Biol. Ecol. 235:147–164.

Sokal, R. R., and F. J. Rohlf. 1987. Introduction to biostatistics. W. H. Freeman and Co., New York.

Uthicke, S., J. A. H. Benzie, and E. Ballment. 1999. Population genetics of the fissiparous holothurian *Stichopus chloronotus* (Aspidochirotida) on the Great Barrier Reef, Australia. Coral Reefs 18:123–132.

Watkinson, A. R., and J. White. 1985. Some life-history consequences of modular constriction in plants. Phil. Trans. R. Soc. Lond. B 313:31–51.

Williams, G. C. 1975. Sex and evolution. Princeton Univ. Press, Princeton, NJ.

Williams, S. L. 1995. Surfgrass (*Phyllospadix torreyi*) reproduction: reproductive phenology, resource allocation and male rarity. Ecology 76:1953–1970.

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