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Sexual Systems and Life History of Barnacles: A Theoretical Perspective

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Synopsis Thoracican barnacles show one of the most diverse sexual systems in animals: hermaphroditism, dioecy (males and females), and androdioecy (males and hermaphrodites). In addition, when present, male barnacles are very small and are called “dwarf males”. The diverse sexual systems and male dwarfism in this taxon have attracted both theoretical and empirical biologists. In this article, we review the theoretical studies on barnacles’ sexual systems in the context of sex allocation and life history theories. We first introduce the sex allocation models by Charnov, especially in relation to the mating group size, and a new expansion of his models is also proposed. We then explain three studies by Yamaguchi et al., who have studied the interaction between sex allocation and life history in barnacles. These studies consistently showed that limited mating opportunity favors androdioecy and dioecy over hermaphroditism. In addition, other factors, such as rates of survival and availability of food, are also important. We discuss the importance of empirical studies testing these predictions and how empirical studies interact with theoretical constructs.

Introduction

The evolution of sexuality is one of the main components of sex allocation theory (Charnov 1982), which aims to elucidate the adaptive strategy of allocation of resources between male and female functions. Sex allocation theory has been studied and tested in various hermaphroditic animals (Schärer 2009), including thoracican barnacles. They show one of the most diverse sexual systems in animals, despite their low locomotive ability (almost immobile after settlement) and uniform mating behavior (copulate with an elongated penis). Most of them are hermaphroditic, but androdioecy (occurrence of males and hermaphrodites) and dioecy (males and females) are known in several species (Darwin 1851). This diversity provides an opportunity for developing and testing theories about evolution of sexuality (Ghiselin 1974; Charnov 1982, 1987; Høeg 1995; Yamaguchi et al. 2008; Kelly and Sanford 2010; Yusa et al. 2012).

When present, male barnacles are always very small and are called “dwarf males”. In this article, we use the term “dwarf male” in a broad sense and define it as males smaller than half the length of conspecific females or hermaphrodites (Vollrath 1998; Yusa et al. 2010). Thus, dwarf males include “complemental” males (males attached to hermaphrodites; Darwin 1851) and “aperiptural” males (those attached to hermaphrodites and having the potential to become hermaphroditic; Crisp 1983). This usage is justified, as no morphological or functional distinctions are suggested between dwarf males (in the narrow sense; attached to females) and complemental or apertural males (Høeg 1995).

While sex allocation theory studies allocation of reproductive resources between male and female functions, life history theory, another branch of
evolutionary ecology, studies allocation of resources between growth and reproduction (Stearns 1992). Dwarf males are animals who adopt a life history strategy that do not invest growth so much, as well as a sex allocation strategy that do not invest female function. Therefore, both sex allocation and life history theories are needed to understand male dwarfism, and hence sexual systems in barnacles (Yamaguchi et al. 2007, 2008, manuscript in preparation). In addition, life history strategy may affect sexuality even without dwarf males, since it determines the structure of mating groups.

In this article, we briefly review the theoretical studies on barnacles’ sexuality. As the literature begins with the sex allocation models by Charnov (1980, 1982, 1987), we first introduce his models, especially in relation to the concept of the mating group size (MGS); a new expansion of his models is also proposed. We then introduce three studies by Yamaguchi et al. (2007, 2008, manuscript in preparation) who have studied the interaction between sex allocation and life history in barnacles. They agree on the role of MGS and the importance of life history strategy.

Overview of models
Sex allocation and mating group size
Charnov (1980, 1982) suggested that the MGS, i.e., the number of large (nondwarf) individuals that can donate sperm to each other, affects sex allocation in sessile animals, such as barnacles. Charnov assumed that each barnacle has R resources to divide between male function (sperm production) and female function (egg production). When the resource allocation to the male function is m, the amount of sperm that each barnacle produces is represented by Rm. Assuming that a mutant barnacle with a male allocation, m, receives sperm from surrounding individuals other than itself, the fitness for the mutant, W, is proportional to the summation of the eggs it reproduces and the eggs it fertilizes, as follows:

\[ W \propto R(1 - \hat{m}) + KR(1 - m) \left( \frac{\hat{m}}{\hat{m} + (K - 1)m} \right), \]

where \( K \) is the number of individuals other than the mutant in a small population, thus MGS = K + 1. To find the evolutionarily stable allocation to the male function \( r^* \) that maximizes the fitness, W, we calculate \( \frac{\partial W}{\partial \hat{m}} = 0 \) when \( r = r^* \).

According to this equation, the evolutionarily stable allocation to the male function by hermaphrodites \( r^* \) increases with \( K \). As \( K \) increases, \( r^* \) approaches to 0.5. When \( K = 1 \), \( r^* \) equals 0, which biologically means that each hermaphrodite produces the amount of sperm that is just enough to fertilize its partner’s eggs when mating occurs only within pairs (Fig. 1).

Proportion of dwarf males in populations with two size-classes
Under the assumption of genetic sex determination, Charnov (1987) constructed another mathematical model to describe the equilibrium proportion of barnacle larvae that become dwarf males. This population consists of two types of individuals with fixed body sizes: large hermaphrodites and dwarf males. At settlement, cyprid larvae are destined to be either large hermaphrodites or dwarf males; future hermaphroditic cyprids compete for open spaces, and future male cyprids compete for special settlement sites on large hermaphrodites. We represent \( q \) as the proportion with which cyprids will be dwarf males. Two factors affect the proportion, \( q \) (equil.), in the population: (1) the ratio of sperm production of large hermaphrodites \( (M_1) \) to that of dwarf males \( (M_2) \) and (2) the maximum number of males each hermaphrodite can accommodate \( (H) \). The proportion, \( q \) (equil.), is

\[ q \text{ (equil.)} = \frac{1}{2} \left( \frac{H \cdot M_2}{H \cdot M_2 + M_1} \right). \]

The proportion \( q \) (equil.) increases and approaches 0.5 as the first factor, \( M_1/M_2 \), decreases to 0 (Fig. 2). Because \( M_1 \) is predicted to be low in small mating groups (see “Sex allocation and mating group size” section), limited opportunity for mating should increase the proportion of dwarf males. Urano et al. (2009) analyzed the effects of MGS on the proportion of dwarf males and on sex allocation in nondwarf individuals in the single model, and obtained similar results.

A new model of natural selection for the evolution of dwarf males
As already indicated, most theoretical studies on the evolution of dwarf males involve a stable proportion of males based on sex allocation theories (e.g.,
Charnov 1987; Urano et al. 2009). Using life history theories, we herein present a simple model of the conditions for the invasion of males when they are very rare. Thus, the origin of androdioecy is the question: under what conditions does natural selection favor a spread of dwarf males introduced into a population of hermaphrodites? We consider dwarf males that do not grow.

Let us consider an hermaphroditic barnacle for \( S / C_1 \), \( E / C_1 \), and \( b / C_2 \), which represent the survival of larvae from hatching to age of first reproduction \( / C_1 \), the average life span of an adult, and the average number of eggs produces per year by an adult, respectively.

Over its lifetime, the hermaphrodite individual will produce

\[
S_a \cdot E_a \cdot \tilde{b} \text{ eggs}
\]  
(see Charnov 1997 for the derivation).

Assuming that all eggs are fertilized, the average number of eggs produced and fertilized by each hermaphrodite is

\[
2 \cdot S_a \cdot E_a \cdot \tilde{b}.
\]  
(2)

This is an hermaphrodite’s lifetime fitness \( W_h \). In a nongrowing population,

\[
S_a \cdot E_a \cdot \tilde{b} = 1,
\]  
(3)
as an individual’s lifetime egg production (net reproductive rate) is just replacement (=1; Charnov 1997). Thus, the average hermaphrodite’s fitness is \( W_h = 2 \).

Let us introduce a rare morph into this population that settles on the mature hermaphrodite and becomes a tiny male who reproduces for \( E \) units of time (\( E \) is much smaller than \( E / C_1 \)). Its lifetime fitness can be written as follows:

\[
E \cdot S \cdot \tilde{b} \cdot \frac{\delta \cdot m}{m + \delta \cdot m},
\]  
(4)

where \( S \) is the survival from larval stage to reproductive age for the male, \( \tilde{b} \) is the average number of eggs produced by the hermaphrodite. \( \delta \cdot m \) represents the number of sperm \( (m) \) from the male multiplied by \( \delta \), which measures how much more likely its sperm is to fertilize eggs, as compared to a sperm from a hermaphrodite, because the male may be in a better location to deliver sperm. The symbol \( \tilde{m} \) is the average number of sperm from each hermaphrodite; thus, \( \delta \cdot m / (\tilde{m} + \delta \cdot m) \) represents the proportion of eggs which are fertilized by the male’s sperm per mating (sperm competition).

When the male morph is rare, it can invade in this population, if Equation (4) > \( W_h \) (=2):

\[
\tilde{b} \cdot E \cdot S \cdot \frac{\delta \cdot m}{m + \delta \cdot m} > 2
\]  
(5a)
or, using Equation (3),

\[
\left( \frac{E}{E_a} \right) \left( \frac{S}{S_a} \right) \left( \frac{\delta \cdot m}{m + \delta \cdot m} \right) > 2.
\]  
(5b)
Males are more likely to be favored if $\tilde{b}$ is high, which means that $S_g \cdot E_g$ is low. $\tilde{b}$ is also expected to be higher if the barnacle population is sparse, as selection then favors relatively greater allocation to the female function $\tilde{b}$ ("Sex allocation and mating group size" section). Interestingly, this will also make $\tilde{m}$ (sperm production by the hermaphrodite) relatively smaller. Thus, a small mating group facilitates selection for males both through the increase in $\tilde{b}$ and the decrease in $\tilde{m}$. In addition, dwarf males are favored if they can donate sperm more efficiently than can hermaphrodites (high $\delta$). Selection also favors the hermaphrodite housing the males because it may otherwise lack mates (Charnov 1987).

**Sexual systems and life history**

Charnov (1987) showed that small barnacles should be males and large ones should be females or hermaphrodites. Although this argument successfully explains the possibility of small males, it cannot exclude the possibility that these males grow into large females (protandric sex change) or hermaphrodites (protandric simultaneous hermaphroditism, PSH; see Schärer 2009). Incorporating growth and subsequent expression of sex is necessary to think of sexuality patterns, whether we call them “dwarf males” or not (see “Discussion” section).

Yamaguchi et al. (2008) constructed a model concerning allocation of resources in barnacles (Fig. 3, Table 1), assuming that a fraction, $c$, of cyprids settle directly on the substratum and the rest on conspecific large individuals. Because conspecific-attached individuals (Con-As) can easily donate sperm to their hosts, small Con-As are assumed to allocate resources to both growth and the male function (sperm production) in the optimal way (reproductive effort as a life history issue). However, we define small substratum-attached individuals (Sub-As, who attach to the sea floor, host animals, floating objects, etc., but not to conspecific barnacles) as those who do not possess a penis long enough to reach other individuals, they are assumed to allocate all of their resources to growth. These constraints are summarized as follows:

$$m_{\text{Con}} + g_{\text{Con}} = 1$$
$$g_{\text{Sub}} = 1$$

where $m_{\text{Con}}$ is the male allocation by a small Con-A, and $g_{\text{Con}}$ and $g_{\text{Sub}}$ are allocations to growth by Con-A and Sub-A, respectively. Both small Con-A and small Sub-A can become hermaphrodites, with a probability in proportion to the amount of resource allocated to growth. Large individuals allocate their resource to male and female functions in the optimal way (sex allocation issue):

$$(\text{Male allocation}) + (\text{Female allocation}) = 1.$$
Conspecific-attached males should grow into large females in spite of low availability of food, as substratum-attached, large individuals are rare. Of the five sexuality patterns, protandric sex change is unknown among barnacles, perhaps because the condition for sex change is rarely realized among them.

In summary, the various sexual systems generally correspond to variations in the MGS. The MGS increases in the order of the following sexuality patterns: (1) dioecy, (2) androdioecy, (3) protandric simultaneous hermaphroditism, and (4) simultaneous hermaphroditism. This agrees with other theoretical (Charnov 1982, 1987; Urano et al. 2009) and empirical studies on barnacles (e.g., Kelly and Sanford 2010; Yusa et al. 2012).

### Sexual systems under continuous growth

Both Charnov (1987) and Yamaguchi et al. (2008) assumed that all individuals are categorized into two discrete size classes: large and small. However, the size distribution in actual organisms is generally continuous. Yamaguchi et al. (manuscript in preparation) studied the evolution of sexuality and life history with continuously growing individuals. These researchers calculated the evolutionarily stable sex allocation and life history of nondwarf (substratum-attached) individuals, together with the stable proportion of dwarf males, under varying environmental parameters (mortality and food availability).

In this model, substratum attached individuals (Sub-As) were allowed to allocate their resources into three outputs (male function, female function, and growth) in the optimal way, according to their body size (size-dependent resource allocation). Nevertheless, mathematical analysis showed that simultaneous allocation to three functions can never be optimal. These Sub-As should become pure females (who invest growth only when small, and female function only when large) or protandric simultaneous hermaphrodites (who invest growth and male function when small, and male and female functions when large). They also calculated the evolutionarily stable proportion of dwarf males. For simplicity, this model does not allow dwarf males (conspecific-attached ones) to grow, as they allocate all of their resources to the male function (Fig. 5).

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**Table 1** Resource-allocation of small individuals (including both those attached to conspecifics and those attached to the substratum) and the sexuality of each type of individual [after Yamaguchi et al. (2008)]

<table>
<thead>
<tr>
<th>Type</th>
<th>Attachment site</th>
<th>Resource allocation to Small</th>
<th>Resource allocation to Large</th>
<th>Sexuality of each individual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Con-A</td>
<td>Conspecific</td>
<td>♀</td>
<td>♀ and ♀ and ♀</td>
<td>Life-long dwarf male</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sex changer</td>
</tr>
<tr>
<td></td>
<td>Growth</td>
<td>♀</td>
<td>♀ and ♀ and ♀</td>
<td>PSH</td>
</tr>
<tr>
<td>Sub-A</td>
<td>Substratum</td>
<td>Growth</td>
<td>♀ and ♀ and ♀</td>
<td>Pure female</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SH</td>
</tr>
</tbody>
</table>

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**Fig. 3** The framework of Yamaguchi et al. (2008). A population consists of two size classes with fixed body sizes: large and small individuals. Large individuals allocate resources to male and female functions (sex allocation), and small individuals allocate resources to growth and the male function (reproductive effort). The sexual system in a population is determined by a combination of the allocation of resources of large and small individuals. MGS is affected by environmental factors, and it, in turn, affects the resource allocation of each type of individual and vice versa.
As a result, the model elucidated how the evolutionary condition of sexual systems depends on environmental factors. When mortality is low, the Sub-As become protandric simultaneous hermaphrodites and dwarf males do not appear, i.e., hermaphroditism evolves. As mortality increases, male allocation by the Sub-As decreases, and the proportion of dwarf males increases, i.e., androdioecy evolves. High mortality leads to dioecy. This result almost agrees with previous studies in the importance of MGS, since high mortality leads to small mating groups. However, under some conditions, pure hermaphroditism evolves despite of small MGS. In these cases, large size of hermaphrodites (as a result of life history strategy) causes an intense sperm competition and prevents the invasion of dwarf males.

The previous model (Yamaguchi et al. 2008; “Sexual systems and life history” section) assumed that both Con-As and Sub-As can potentially reproduce and grow in a population with discrete size classes. The current model successfully studied a
population with continuously growing Sub-As, assuming Con-As do not grow. Obviously, models in which both Sub-As and Con-As grow continuously are required. Although such models have not been constructed yet, growth strategy of dwarf males was theoretically studied by Yamaguchi et al. (2007). This is the topic of the next section.

**Life history of dwarf males**

Charnov (1987) suggested that the sperm production of a large barnacle relative to that of a dwarf male ($M_1/M_2$) is the key factor for invasion by dwarf males. It is reasonable to assume that the amount of sperm that a dwarf male produces depends on its body size. Nevertheless, most theoretical studies assume the size of dwarf males to be constant (Charnov 1987; Yamaguchi et al. 2008, manuscript in preparation; Urano et al. 2009). Because there is a considerable inter-specific variation in the size of dwarf males among barnacles (Pilsbry 1908; Buhl-Mortensen and Høeg 2006), the body size of dwarf males should affect the evolution of barnacles’ sexuality.

Yamaguchi et al. (2007) studied the evolution of variation in size among dwarf males by analyzing their evolutionarily stable life history strategy under varying intensities of sperm competition and amounts of food and found that intense sperm competition and abundant food lead to relatively large dwarf males. It is predicted that (1) males in androdioecious species are larger than those in dioecious species, as the former face sperm competition with sperm-producing hermaphrodites, and (2) dwarf males in food-poor habitats, such as the depths of the sea, are small and often do not grow at all (Fig. 6). The prediction (1) is supported by a preliminary analysis by Yusa and Yamato (unpublished data), whereas the prediction (2) is supported by the existence of nonfeeding dwarf males in deep-sea barnacles (Buhl-Mortensen and Høeg 2006; Ozaki et al. 2008). However, both predictions require more comprehensive and systematic empirical testing.

**Summary and discussion**

The above theories suggest roles both for sexual selection (sperm competition) and natural selection (life history strategies) in the evolution of sexuality in barnacles. Small mating groups enhance the competition among sperm from one hermaphrodite (local sperm competition; Schärer 2009). Because such competition is wasteful for sperm donors, it decreases male allocation by hermaphrodites. If the mating group is small enough, the male allocation of hermaphrodites becomes zero; i.e., pure females evolve. However, as dwarf males are miniscule and therefore produce only a small amount of sperm, it is difficult for them to achieve sufficient success in fertilization under intense sperm competition. Thus, the evolution of dwarf males is enabled by two factors: (1) decreased male allocation by hermaphrodites in small mating groups and (2) efficient sperm transfer for dwarf males, possible because of their close proximity to females. In addition, male dwarfism may be an adaptive life history strategy under some environmental conditions, such as high mortality and scarcity of food, which favor early maturation and little growth.

The above predictions must be tested against empirical evidence. In addition, such empirical data will clarify the need for further theoretical studies. In the following sections, we discuss empirical studies of barnacle sex allocation in relation to the theories described above. First, we discuss the empirical studies on the relationship between sex allocation and MGS and the future relevant theoretical work required. Second, we address the empirical data on sexual systems and their feedback to theoretical work. We do not intend a comprehensive review of such studies; readers should consult Kelly and Sanford (2010) for further information.
Sex allocation and mating group size

The relationship between sex allocation and MGS predicted by Charnov (1980, 1982) was tested by several studies using various hermaphroditic animals (Schärer 2009), including barnacles. Raimondi and Martin (1991) found a positive relationship between the relative allocation to male and female functions and the MGS in an hermaphroditic barnacle, Catomerus polymerus, clearly supporting the prediction of Charnov. However, the results of other studies are not as clear. Kelly and Sanford (2010) did not find any significant relationship between MGS and the allocation to male and female functions in another hermaphroditic barnacle, Tetractita rubescens. Hoch and Levinton (2012) conducted an experimental manipulation of density and crowding, using two hermaphroditic species, and found that the allocation between male and female functions was not affected by density or crowding. These authors suggested that male allocation is limited by the brood space as determined by the body size and body shape in Semibalanus balanoides. This suggestion is interesting because limitation of brood space is predicted to facilitate the evolution of hermaphroditism (Heath 1977) and male-biased sex allocation (Charnov 1982). However, this factor is not explored by the models explained above, as they assume a linear gain in fitness for female function. These empirical studies focused on variations at the individual level that are caused by phenotypically plastic responses to local environments (i.e., environmentally determined sex allocation). However, most theoretical models of sex allocation, including those explained above, analyze a single optimum under uniform environmental conditions (i.e., genetically determined allocation) and primarily focus on species-level or population-level variations. Although they often roughly agree, these two approaches are not necessarily equivalent (Schärer 2009). Models on plastic sex allocation and empirical studies on inter-specific variation are both required for a better interaction between the theoretical and empirical studies.

Evolution of sexual systems in barnacles

Three studies mentioned in “Sex allocation and mating group size” section (Raimondi and Martin 1991; Kelly and Sanford 2010; Hoch and Levinton 2012) used purely hermaphroditic species only; thus, they do not directly address sexual systems, even though they test key assumptions of models on sexuality. It would be interesting to conduct such a study using androdioecious barnacles, especially those with variations in the abundance of dwarf males. Intra-specific variation in presence or absence of dwarf males (e.g., in Octolasmis warwickii; Jeffries et al. 1989; Yusa et al. 2010) may also provide a good opportunity to test such theories. It is predicted that dwarf males tend to appear when hermaphrodites allocate less resources to male function.

Although sexual systems appear to be phylogenetically constrained in some animal taxa (Schärer 2009), it is unusually labile in barnacles (Kelly and Sanford 2010), enabling inter-specific comparisons. Some factors, such as depth of water or symbiosis, are suggested to be correlated with inter-specific variation in sexual systems. For example, dwarf males are observed to be common in deep-sea scalpel lids (Newman 1980; Buhl-Mortensen and Høeg 2006; Ozaki et al. 2008), a trend that provides support for the importance of abundance of food as suggested by Yamaguchi et al. (2008, manuscript in preparation), because food is generally scarce deep in the sea (Herring 2001). This observation is also consistent with the effect of MGS, as deep-sea species tend to be sparse (Buhl-Mortensen and Høeg 2006; Yusa et al. 2012); see Kelly and Sanford (2010) for further discussion of these patterns.

Comprehensive comparisons of sexual systems in barnacles with a statistical control of phylogenetic relationships (Felsenstein 1985) are almost absent. The only exception is this study by Yusa et al. (2012) who examined the relationship between opportunity for mating (as indicated by the proportion of isolated nondwarf individuals) and sexual systems (the presence or absence of dwarf males and of pure females) in pedunculate barnacles, using a phylogenetic comparative method. These authors found that dwarf males and pure females tend to evolve in lineages with many isolated individuals, a result that strongly supports the importance of MGS. Such comparative studies are show promise for the elucidation of the evolution of sexual systems. Especially, hypotheses that ecological factors (depth, symbiosis, and so on) affect sexual systems should be tested by phylogenetic comparative methods.

Some authors argued the ambiguity of the distinction between androdioecy and hermaphroditism in barnacles (Kelly and Sanford 2010; Yusa et al. 2010), as it has been suggested that dwarf males possess the potential to grow into functional hermaphrodites in some barnacle species (Crisp 1983;
If so, these dwarf males are not pure males but are protandric simultaneous hermaphrodites arrested at the male stage. Yusa et al. (2012) considered these as “dwarf males” for the following three reasons: (1) they attach to specific sites of conspecifics, (2) they allocate more resources to the male function than do normal hermaphrodites, and (3) they have little, if any, possibility of becoming functional hermaphrodites. The third criterion depends on the fact that the potential of such a transition seems to be small [e.g., Yusa et al. (2010) found only four conspecific-attached hermaphrodites of 34 conspecific-attached barnacles]. If barnacles with various transitional possibilities were discovered, we would have to consider that typical androdioecy and pure hermaphroditism are different ends of the spectrum (Yusa et al. 2010). Importantly, Yamaguchi et al. (2008) suggested such a continuum of transitional probabilities under varying abundances of food. Indeed, the presence of potentially hermaphroditic dwarf males is not just a matter of terminology but suggests another way of achieving fitness for “dwarf males”: it may be a good solution under unpredictable ecological/social conditions to be a dwarf male first and then become a hermaphrodite if possible. The importance of protandric “dwarf males” is not fully explored, either theoretically or empirically.

Along with potential hermaphroditism, the growth of dwarf males is an interesting factor that has not been fully studied. Although defined by their smallness, dwarf males indeed become considerably large in some species (Annandale 1905; Hiro 1933). In contrast, dwarf males in other species are extremely small and of reduced form, without feeding organs, and do not grow at all (Nilsson-Cantell 1931; Klepal 1987; Buhl-Mortensen and Høeg 2006; Ozaki et al. 2008). Yamaguchi et al. (2007) considered the size and growth of dwarf males as part of a life history strategy. However, no theoretical studies have examined the relationship between the conditions for growth and the evolution of dwarf males. On the one hand, the growth of dwarf males enables them to produce sufficient amounts of sperm to be competitive; from this perspective, dwarf males are predicted to be larger under intense sperm competition (Yamaguchi et al. 2007). On the other hand, growing may reduce the advantage that dwarf males derive from their smallness, such as early maturation (Zardus and Hadfield 2004; Yusa et al. 2010). Both protandry and the growth of dwarf males necessitate study of the whole life history.

**Why do barnacles have diverse sexual systems?**

Since the primary focus of these models is the distribution of various sexual systems within barnacles, they do not directly explain why barnacles have so diverse systems compared to other animals. However, these models offer some implication on this question. Weeks et al. (2006) pointed that hermaphrodites do not mate each other and use their sperm exclusively for self-fertilization in all androdioecious animals other than barnacles. If this is the case, the variation in MGS, which is predicted to underlie diverse sexual systems of barnacles, cannot exist among those animals. This constraint may prevent the evolutionary transition between dioecy and pure hermaphroditism through androdioecious transitional states. Another possible factor is the advantage of dwarf males in sperm donation (δ in “A new model of natural selection for the evolution of dwarf males” section). The attachment to hermaphrodites makes dwarf males advantageous in sperm competition and can facilitate the evolution of androdioecy from hermaphroditism. From this view, it is interesting that dwarf males in dioecious animals often live on females (Vollrath 1998). However, no quantitative measurement of the advantage of attachment in sperm competition is available to date.

**Conclusion**

The concept of MGS, as suggested by Charnov in the 1980s, continues to play an important role both in theoretical and empirical studies of barnacles’ sexuality. However, other factors, especially life history strategies, should not be ignored.

Barnacles have several characteristics that are favorable for evolutionary ecologists who are interested in evolution of sexual systems, including the evolutionary flexibility of sexuality, the immobility that enables field estimations of opportunity for mating, and accumulation of knowledge about natural history. We believe that the studies of the sexuality of this taxon will constitute a model case for an ideal collaboration between theoretical and empirical biologists.

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