Using potential reproductive rates to predict mating competition among individuals qualified to mate

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The potential reproductive rate (PRR), which is the offspring production per unit time each sex would achieve if unconstrained by mate availability, often differs between the sexes. An increasing sexual difference in PRR predicts an intensified mating competition among the sex with the higher PRR. The use of PRR can provide detailed predictions of when, where, and how the intensity in mating competition and hence sexual selection will vary. Previous models have focused on the “time out” from mate searching as a major component of PRR. Here, we suggest some improvements and clarifications: in a population where individuals have to compete for specific resources that are prerequisites for mating (e.g., nest sites), individuals unable to obtain such a resource will not qualify to mate. We suggest how a concept of the ratio of males and females qualified to mate, Q, can improve previous models designed to use the sexual difference in PRR to estimate the operational sex ratio (OSR). Further, when estimating the sexual difference in PRR of a population, it is important that each sex is given free access to mating partners. Jointly, this provides an empirical approach based on estimates of Q and the sexual difference in PRR. Key words: mating competition, operational sex ratio, OSR, adult sex ratio, potential reproductive rate, PRR, qualified to mate, resource competition. [Behav Ecol 12:397–401 (2001)]

A prominent explanatory model for predicting the direction and intensity of competition for access to mates is based on the sexual difference in potential reproductive rates (PRR; Andersson, 1994; Clutton-Brock and Parker, 1992; Kvarnemo and Ahnesjö, 1996; Parker and Simmons, 1996; Reynolds, 1996), where PRR is the potential offspring production per unit time. There is a close association between PRR (Clutton-Brock and Parker, 1992; Kvarnemo and Ahnesjö, 1996; Parker and Simmons, 1996) and the operational sex ratio (OSR; the ratio of sexually active males and females at a given time and place; Emlen, 1976; Emlen and Oring, 1977). A sexual difference in PRR will shift the OSR toward the potentially faster reproducing sex. Together with PRR, the sex ratio in the mating pool will obviously also influence the OSR.

The traditional explanation for why males, more often than females, compete for access to mating partners, is that females invest more than males in reproduction (Trivers, 1972). However, this has proven difficult to test because any measurement of parental investment should include all fitness costs of all expenditures of reproduction in both sexes (Clutton-Brock, 1991; Evans, 1990; Knapton, 1984). Therefore, we argue like several authors before us (Clutton-Brock and Parker, 1992; Clutton-Brock and Vincent, 1991; Parker and Simmons, 1996) that a more accessible empirical approach is to measure the sexual difference in PRR of a population and then estimate the OSR. Not only does this approach provide an estimate of OSR and mating competition, but also an avenue for understanding the mechanisms governing spatial and temporal variations in OSR. The advantages of using PRR are becoming increasingly recognized (e.g., Ahnesjö, 1995; Balshine-Earn, 1996; Berglund et al., 1989; Debuse et al., 1999; Kvarnemo, 1994; Masonjones and Lewis 2000; Okuda, 1999; Pröhl and Hödl, 1999; Simmons, 1995; Wiklund et al., 1998; Wootton et al., 1995). In this paper we aim to promote further use of PRR by clarifying and developing some of its important aspects.

In a population, sexual selection may occur for many reasons, such as mating competition, resource competition, and sperm competition. Out of these, it is only mating competition that can be estimated by a sexual difference in PRR and any consequent bias in OSR. In contrast, when resources (other than mates) that are prerequisites for mating are limited, competition for these resources will occur. Although such resource competition may result in sexual selection, it will not be predicted by any sexual difference in PRR. Nor will sperm competition, which occurs after mating, be predicted by models using PRR, and possible indirect effects of sperm competition on PRR have been found to be of minor importance (Simmons and Parker, 1996). In addition, prominent variation in mate quality may result in competition for high-quality mates. Yet, its influence on mating competition has been predicted to be minor in comparison to that of sex differences in PRR (Johnstone et al., 1996) and will not be considered further in this paper.

There are several important factors that need to be considered to predict and understand mating competition. First, there is a need to understand the consequences of resource competition on mating competition without confounding these two, and we suggest how this can be incorporated by identifying the ratio of males and females qualified to mate (i.e., those able to enter the mating pool) when using PRR to...
Figure 1
To illustrate the influence of resource limitation on mating competition, we first picture the adult sex ratio (ASR; M in Parker and Simmons, 1996) in a population of seven males and seven females. All females produce eggs, but due to resource limitations, only four of the seven males are able to acquire a certain resource that is necessary for reproduction (e.g., a nest site). This results in Q (the sex ratio between males and females qualified to mate), which in turn is the outset for mating competition among these individuals. For simplicity, we assume that each individual only mates with one partner. If three of the females mate with three of the males, they will all be in time out, caring for offspring and replenishing gametes. However, there will still be four unmated females in time in, which will have to compete for one unmated time-in male, resulting in a female-biased operational sex ratio (OSR). As a consequence, females are predicted to be the sex that predominantly competes for mates. Yet, to understand the scenario for a whole reproductive event or cycle, one has to include the potential reproductive rate (PRR) for each sex, which is the production of offspring per unit time when unconstrained by mates. PRR should only be calculated for individuals included in Q and then OSR = Q̃PRR/PRR.

estimate the OSR in a population. Second, PRR has been approached in several ways, resulting in slightly different definitions and estimates, based on different assumptions, which we will try to clarify. Third, we outline a general empirical approach estimating the OSR by the use of the sexual difference in PRR among the individuals qualified to mate.

The sex ratio of males and females qualified to mate
Previous calculations and models of PRR and OSR have generally been based on the adult sex ratio (e.g., Clutton-Brock and Parker, 1992; Parker and Simmons, 1996). However, as mentioned by Clutton-Brock and Parker (1992), this may sometimes cause problems. To illustrate our point, imagine a species where the adult sex ratio is even and individuals of one sex construct a nest and then provide care for the offspring. For simplicity, we also assume that the “time out” periods (time between matings spent not ready to mate; see the time-out model below) or a “time out” state. To enter time in (and time out following it), an individual must first acquire the resources that are a prerequisite for mating, such as a nest site (Figure 1). A nest holder can thus be considered qualified if it is potentially eligible as a mate (whether this will be realized or not). In contrast, an individual that has not acquired a nest site is not eligible as a mate, even though it might be capable of mating through sneaking. In more general terms, prerequisites for mating may include breeding and feeding territories, as well as nutritive resources, such as nuptial gifts. There is a distinction between those individuals being unable to acquire resources (food, for instance) to become qualified to mate and those that have started mating and are drained of resources after a mating. The former individuals are excluded from Q whereas the latter are qualified to mate, although they are in their time-out state.

One will gain a major advantage replacing the adult sex ratio with Q because estimates of mating competition no longer will be confounded or masked by resource competition. An example of the distinction between resource competition and mating competition is provided, for instance, by a study of the Pacific salmon, Oncorhynchus kisutch (Fleming and Gross, 1994). In this species, females were found to compete
for oviposition territories, and smaller females were less successful in acquiring and defending such territories. As a result, males faced an intense mating competition for access to the territorial females, favoring male body size and hooked snout length. Further, \( Q \) can be compared to the adult sex ratio to detect resource competition within a sex and to predict the intensity of resource competition. Emlen and Oring (1977: 217) dealt with the question of how resources may influence mating systems and sexual selection. They described it as resource-defense polygyny when "males control access to females indirectly, by monopolizing critical resources," and vice versa for resource defense polyandry. In such resource-defense polygyny, an individual that holds a critical resource may enjoy a mating advantage. Still, if the number of mates the resource holder can have is limited, the degree of polygamy may remain low. Although Emlen and Oring (1977) focused on the competition among the resource-holding sex, they did not pay attention to the mating competition that may arise among the opposite sex for the resource-holding individuals.

Some further examples from fish research illustrate the situation where the adult sex ratio differs from \( Q \). In the peacock blenny \( Salaria pavo \), males provide parental care in nest sites in rock crevices. In most populations, males compete for and court females. However, the reverse was found in a population in Portugal (Almada, 1995). The only substrates available in this case were old construction bricks that lined the edges of man-made water channels. Although excellent nest sites, these bricks were limited in numbers. Hence, in this population, the OSR was female biased because only a small proportion of the males were able to acquire a nest, whereas all females were producing eggs (Almada, 1995; Oliveira et al., 1999). As a consequence, and despite an intense competition for nest sites among males, the sex roles were reversed in this population, with females being more keen competitors for mates than were males.

The influence of nest site availability on sexual selection has also been studied in two species of gobies, \( Pomatoschistus minutus \) and \( P. microps \), both of which provide exclusive parental care in nests built under mussel shells. In \( P. minutus \), male mating success was primarily determined by intrasexual competition over nest sites (i.e., resource competition) when nest sites were in shortage. In contrast, when nest sites were available in excess, male mating success was determined to a larger extent by female mate choice (Forsgren et al., 1996). In \( P. microps \), females interacted with each other and courted more than males did when nest sites were limiting, whereas the reversed was true in an area with excess nests (Borg Å., Forsgren E., Magnhagen C., personal communication). These differences show that since nest site availability affects \( Q \) and therefore OSR, it will also affect the modes of sexual selection, from intrasexual resource competition to intersexual mate choice.

The potential reproductive rate

Potential reproductive rate is a measure of offspring productivity per unit time of individuals that are not constrained by availability of mating partners (Clutton-Brock and Parker, 1992; Kvarnemo and Ahnesjö, 1996). As a consequence of this criterion of unconstrained access to mating partners, PRR usually differs from the realized reproductive rates we see in natural populations. In any sexually reproducing organism, the mean values of the realized reproductive rates of males and females will be equal, as each offspring has one mother and one father. Therefore, PRR cannot be measured in unmanipulated field conditions where focal individuals cannot be guaranteed unlimited access to mates.

There are examples where PRR has been estimated in the field, using measurements for each sex of the time-out periods after one mating (e.g., Okuda, 1999; Pröhl and Hödl, 1999). Sometimes this is the only feasible way to get a rough estimate of PRR. Yet, by not providing free access to mates, one is likely to overestimate the time out of the limited sex if it does not appear to be ready to remate due to the lack of mating partners. In other cases, there may be a risk of underestimating the time out if recovery and replenishment occurs during searching for a new mate. Finally, it is not unusual that one sex is prepared to mate several times in rapid sequence before spending the required time for recovery. In such a case, by only measuring time out from one mating, PRR is likely to be inaccurately estimated for this sex. In contrast, by providing unlimited access to mates, as stressed above, one is able to accurately estimate the physiological and ecological upper limit of the rate at which each sex, on average, potentially can reproduce.

Clutton-Brock and Vincent (1991) coined the term “potential reproductive rate,” but illustrated it by using the maximum value of the realized reproductive rates recorded in the literature for a range of species. Although having a heuristic value as an example, this method gives an unreliable estimate because it is not known how it relates to PRR. Moreover, subsequent empirical studies (e.g., Balshine-Earn, 1996) have measured the potential reproductive rates for a range of individuals within a population, but then only used the maximum individual value of each sex to estimate PRR instead of the mean. As a consequence, this estimate is not reliable for the calculation of OSR because it does not statistically represent all the individuals in the population for which mating competition is measured, but only one extreme male and one extreme female.

The time-out model

When individuals are ready to mate, they are said to be in a "time-in" state. In contrast, when they have mated and as a result spend time caring, replenishing gametes, or recovering somatically before being ready to mate again, they are said to be in a "time-out" state (Clutton-Brock and Parker, 1992; Parker and Simmons, 1996). This also relates to previous divisions of reproductive time into two categories (searching time and mating time; Sutherland 1985; Sutherland and De Jong 1991). The underlying concept for the time-out model is that the OSR is equivalent to the sexes' ratio of summed time-in periods in a population (Clutton-Brock and Parker, 1992). However, because time-in is hard to measure, the model compares the sexes' time-out periods instead (Parker and Simsmons, 1996). Assuming discrete clutches, Clutton-Brock and Parker (1992) and Parker and Simmons (1996) divided the reproductive cycle \( T \) of each sex into time out \( G \) from mate searching, when not being ready to mate, and time in \( S \) when being ready to mate. The three main determinants of OSR and hence mating competition in these models are (1) the sex ratio of adult individuals \( M/f \); males/females \( (2) \) the inverse time out, \( 1/G \); and (3) the "collateral investment" (sensu Parker and Simmons 1996). The quotients \( G^G \) and the collateral investment together correspond to PRR: \( 1/G \) is a time component, whereas the collateral investment translates into the potential number of offspring the sexes have capacities to produce or take care of during the period of \( G \). Collateral investment occurs if a given reproductive event involves the time-out periods of more than one individual of each sex, such that \( f \) females spread their clutches between \( m \) males (Parker and Simmons, 1996). For example, if a male has the capacity to care for eggs from two or more females in his nest at one time, as is common among fish with paternal care, then the collateral investments are \( m \geq 2 \) and \( f = 1 \). Alternatively,
if two or more males mate with one female before oviposition, as is common in katydids and butterflies, each of the two males will spend a time out, replenishing their sperm stores and nuptial gifts, for only one female time out. Here, the collateral investments are \( m = 1 \) and \( f \geq 2 \). It is important to note that the estimates of collateral investment must be based on how the time-out periods would be distributed under free access to mates, in order to, for instance, know the maximum number of clutches that may fit into each individual nest (cf. Kvarnemo, 1994).

When using the model by Parker and Simmons (1996), it is not arbitrary if we specify the reproductive cycle \( T \) (total time in which an entire reproductive event takes place for one sex) for the limited or limiting sex. It is advisable to use the reproductive cycle \( T \) and clutch size for the limiting sex. If choosing \( T \) for the limited sex, one will have to do adjustments, for instance, by only using fractions of time-out periods for the other limiting sex.

Keeping the above reservations in mind, a reproductive cycle \( T \) can be defined as \( T = \frac{mG}{fG} + S \) when females are the limiting sex, and males are then expected to compete if \( T(Q - 1) > mG_f - fG \) [here replacing the adult sex ratio, \( M \) (Parker and Simmons, 1996) with \( Q \) see above]. However, more information can be gained beyond which sex is the predominant competitor for access to mates, as the difference in the inequality gives an indication of the intensity of mating competition in the population (Emlen and Oring, 1977; Kvarnemo and Ahnesjö, 1996; Kvarnemo and Ahnesjö, in press).

Parker and Simmons (1996) approached PRR by separating it into the inverse processing time of a clutch (i.e., \( 1/G \)) and the capacity to process multiple time-out periods of the opposite sex within a reproductive cycle (i.e., collateral investment). In some species, this is likely to be a useful approach to determine what governs certain changes in OSR. In such species the reproductive cycle \( T \) can easily be defined, and a mating involves an entire clutch, or a nuptial gift, inflicting time out after a certain number of matings, as has been demonstrated in sand gobies (Kvarnemo, 1994) and katydids (Simmons, 1995). In many other species, the reproductive cycle is harder to determine, and the separation of PRR into time and collateral investment will be unfeasible. A better approach is then to measure PRR as the number of offspring produced per unit time under free access to mates, thus incorporating both time out and collateral investment in the same estimate. This is a more general approach, which is applicable both to species reproducing more or less continuously for a period and to clutch-wise reproducers. This approach could be seen as the original one, as it follows the verbal definition of PRR in Clutton-Brock and Parker (1992), which in turn was based on studies that were fundamental to the development of the concept (Berglund et al., 1989; Gwynne, 1984).

An empirical approach

When surveying a population of animals, it may be difficult to collect estimates of the factors used in the above models (e.g., mean time-out periods or the summed time-in periods, level of potential collateral investments, and the ratio of males and females qualified to mate). In many cases it is more feasible to bring representative samples of the population into the laboratory (or field enclosures), separately provide individuals of both sexes with free access to mates, and then measure the rate of offspring production. Often, a suitable minimum time period for the measurements is the duration of one reproductive cycle of the slower sex. This will provide a mean PRR for each sex, and the sexual difference can be calculated and used to predict intensities of mating competition (Clutton-Brock and Parker, 1992; Kvarnemo and Ahnesjö, 1996). For the slower sex, mean PRR is likely to equal its realized reproductive rate, whereas the faster sex will have a higher mean reproductive rate when not being limited by the availability of partners.

Thus an outline for an empirical approach for estimating the OSR by the use of \( Q \) and PRR is as follows:

1. To estimate \( Q \) determine the ratio of males to females that qualify to mate, either directly in the field, or by taking a representative sample of the population into the laboratory or field enclosures. In the laboratory it is important to maintain the adult sex ratio, spatial distribution, size and age distribution and to provide natural levels of resources (food, nests, etc., limited or unlimited in amount depending on what occurs in nature).

2. Determine the mean PRR for each sex separately by first determining how many offspring each individual produces when provided with continuous free access to mates but all the other natural constraints remain, measured under a suitable time period (e.g., a reproductive cycle of the slower sex). Then calculate PRR for each sex as the average number of offspring produced per unit time in the sample.

3. Multiply \( Q \) by the ratio of male PRR to female PRR to obtain OSR. As previously suggested (Kvarnemo and Ahnesjö, 1996), it is preferable to transform the OSR estimates to a relative form (e.g., ranging from 0–1 or as a percentage 0–100%) to avoid the skewed distributions characteristic of a male to female ratio.

4. An OSR departing from unity (i.e., 0.5) will then predict more intense competition for access to mates in the faster sex or the sex with more individuals qualified to mate.

5. If the study focuses on seasonal changes in mating competition, these estimates have to be repeated sequentially over the breeding season.

This approach has been successfully used in a sex-role reversed population of the broad-nosed pipefish, Syngnathus typhle. In this species \( Q \) is even, but females have to compete for males as mating partners because, on average, females are able to produce eggs twice as fast as males are able to brood them (Ahnesjö, 1995; Berglund et al., 1989), resulting in female-biased OSRs over the main part of the breeding season (Vincent et al., 1994).

Discussion and conclusion

When there is competition among members of one sex for resources that are prerequisites to mate, some individuals will qualify to mate, whereas others (although being sexually mature) will not. At the onset of the breeding season, the ratio of males to females qualified to mate \( (Q) \) is likely to approximate OSR. Thereafter individuals will be ready to mate or not depending on their PRR. Consequently, the OSR will vary over time. Naturally, \( Q \) may also change as new individuals become qualified to mate. We emphasize here that for each sex the PRR estimates the reproductive rate of all the mating individuals when they are not constrained by mate availability, but all other natural constraints remain. Kvarnemo and Ahnesjö (1996) have stated that nest site limitation among males may cause a female-biased OSR through a reduction of PRR of the nest-holding sex. This would be the case if males without a nest were assigned an individual PRR value of zero, thereby decreasing the population mean PRR for males. However, assigning zeros for nestless males implies that they spend infinite time in a time-out state. Although mathematically practicable, this is illogical because time-out can only result from a mating, and a male without a nest is neither in a time-in nor a time-out state. In addition, not including zeros for these individuals keeps PRR an unambiguous measure of the potential rate of processing gametes and offspring. Con-
sequently, for both the empirical approach and the time-out model we clearly prefer the approach of $Q$ because it allows PRR to be measured only for the individuals qualified to mate. Thus, an estimate of a population’s OSR is acquired by combining information on $Q$ and the sexual difference in PRR. Any change in $Q$ and the sexual difference in PRR affects the OSR, in the same or opposite directions. Hence, male–male competition will predominantly occur when females limit male reproduction due to more males than females being qualified to mate or due to males having a higher PRR. Sex-role reversal with female–female competition for access to mates will occur in opposite situations. Further, the relationship between the bias in OSR and the intensity of mating competition is not necessarily linear, as costs and benefits of competitive behavior may vary with the degree of bias in the OSR. For instance, when the OSR is strongly biased toward one sex, the costs of competition may become very high and the intensity may then decrease, as suggested for the European lobster (Debuse et al., 1999).

The empirical outline presented above should be seen as complementary to previous approaches. Although the OSR sometimes can be successfully estimated directly by counting individuals of both sexes that are ready to mate, it is often difficult to assess when an individual is ready to mate. Furthermore, to determine the mating competition over a mating period the OSR count will have to be repeated frequently. The time-out model (Parker and Simmons, 1996) serves as another alternative, which is excellent from a theoretical perspective. This model compares the summed time-in periods between the sexes over a reproductive cycle, but because it is often difficult to assess if individuals are in a time-in state, the model uses estimates of time out instead. Yet, when incorporating the effects of sex-ratio biases, it is crucial to use the sex ratio of qualified individuals ($Q$) and not of all adult individuals ($M$). In addition, effects of collateral investments (i.e., when a reproductive event involves the time out of more than one mating partner) have to be included (Parker and Simmons, 1996). The empirical outline presented in this paper circumvents several of the problems related to the time-out model by estimating $Q$ and the sexual difference in PRR to calculate the OSR. Furthermore, focusing on PRR enables us to identify the factors that more prominently influence OSR. Using information about how such key factors vary may help us produce predictions about mating competition in different populations or for different times of the breeding seasons. The improvements and clarifications suggested here will facilitate accurate estimates of mating competition when conditions vary within and between populations.

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