Available online at www.sciencedirect.com

ScienceDirect

Theoretical Population Biology 73 (2008) 112–124

Theoretical Population Biology

www.elsevier.com/locate/tpb

Understanding mating systems: A mathematical model of the pair formation process

Aline Magdalena Lee[a,*], Steinar Engen[b], Bernt-Erik Sæther[a]

[a]Centre for Conservation Biology, Department of Biology, Norwegian University of Science and Technology, Realfagsbygget, N-7491 Trondheim, Norway
[b]Centre for Conservation Biology, Department of Mathematical Sciences, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

Received 29 March 2007
Available online 4 October 2007

Abstract

Mechanisms generating inequalities among males in reproductive success are key to understanding the evolutionary significance of sexual selection. This paper develops a stochastic model to quantitatively describe and analyze mating systems on a continuous scale from strict monogamy to extreme polygyny. The variance in male mating success is shown to increase with increased differences among males, with decreased interdependence of mating events, with increased population size, and with an increased number of females per male. The latter condition decreases the opportunity for sexual selection. It is found that different combinations of mating system characteristics can lead to the same variance in male mating success, although the distribution differs. This emphasizes the importance of using a model of this type to study mating systems, rather than relying solely on the variance in reproductive success as a descriptor of different systems.

Keywords: Mating systems; Pair formation; Reproductive skew; Reproductive success; Sexual selection; Stochastic model

1. Introduction

The differences between males and females within animal species are many and diverse. One major difference is that females produce energy rich eggs while males produce relatively cheap sperm (Wallace et al., 1996). Therefore, a single male has the capacity to produce large numbers of gametes and fertilize the eggs of many females. A female only needs one or a few mates to accomplish fertilization of her eggs. This means that female reproductive success is usually limited by access to resources, whereas male reproductive success is often limited by access to mates (Bateman, 1948). Because of this, females are assumed to be choosy when selecting mates, whereas males are expected to mate with as many females as possible (Bateman, 1948). The resulting sexual conflict, working within the boundaries of ecological factors and physiological constraints of different species, has led to a wide variety of mating systems (Trivers, 1972). It has, however, been shown that a large variance in mating success among males does not necessarily indicate non-random mating (Sutherland, 1985). The most basic distinction among mating systems is the number of mates individuals of each sex may have in a breeding season (Thornhill and Alcock, 1983), how the pair formation takes place (Emlen and Oring, 1977), and how much individuals of each sex invest in parental care (Trivers, 1972; Krebs and Davies, 1993).

Although mating systems vary significantly in most taxa (e.g. Davies, 1991), the processes involved in generating the differences are still poorly understood. The contributing factors seem to be many and complicated (Andersson, 1994). In one influential paper, Emlen and Oring (1977) suggested that an important cause of the variation in mating systems is the extent to which potential mates are economically monopolizable. They hypothesized that the average ratio of sexually receptive females to sexually active males present in a population at any given time (termed the operational sex ratio, OSR) can be used as a measure of the monopolizability of mates, and thus of the

---

*Corresponding author.

E-mail addresses: aline.lee@bio.ntnu.no (A.M. Lee), steinaen@math.ntnu.no (S. Engen), Bernt-Erik.Sather@bio.ntnu.no (B.-E. Sæther).

0040-5809/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.tpb.2007.09.003

degree of polygamy (polygyny or polyandry) in the population.

In the present paper it is proposed that the potential degree of polygamy can be modeled by the strength of interdependence of matings. If individuals that have already mated once have no possibility of mating again, interdependence of matings is very strong and the mating system is monogamous. At the other extreme, a population in which mating events are totally independent will have the potential for extreme polygamy. In this case the mating chances of individuals will not be affected at all by the number of matings they have already participated in. This concept is closely related to the economic monopolizability of mates described by Emlen and Oring (1977).

Differences in mating systems are intimately linked with the intensity of sexual selection (Emlen and Oring, 1977), described by Darwin (1875, p. 209) as "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction". Sexual selection is an important source of evolutionary change in natural populations (Shuster and Wade, 2003). The potential reproductive rate (PRR) of males and females has been suggested as a predictor of the direction of sexual selection, and is defined as the maximum number of independent offspring an individual of a given sex can produce per unit time (Clutton-Brock and Vincent, 1991). A frequently used measure of the opportunity for sexual selection is the variance in mating success divided by the mean mating success ($\mathrm{Var}(X)/\bar{X}^2$) (Crow, 1958; Wade and Arnold, 1980). This measure sets an upper limit for the intensity of sexual selection (Wade and Arnold, 1980; Arnold and Wade, 1984).

Darwin (1875) pointed out that in order for sexual selection to act in monogamous species, some individuals must gain a reproductive advantage over others with the same number of mates. Darwin (1875) and Fisher (1958) suggested that superior males gain access to the first females ready to mate in a season, and that these females should be more vigorous, and thus produce more offspring than later breeding females, thereby allowing the superior males a reproductive advantage. Generalizing this idea, a decomposition of mating systems by Arnold and Duvall (1994) and Møller (1994b) identified two main paths of sexual selection: differential mating success and differential fecundity per mate. Each of these pathways has a number of contributing factors (e.g. search and handling time, parental investment and infanticide). The concept of male mating success is more complicated than it may appear on the surface. Multiple mating by females and sperm competition is common in natural populations (Birkhead and Møller, 1998). Gaining access to mates may therefore not guarantee a male paternity.

One proposed way of quantifying inequalities in reproductive success is with a reproductive skew index. Several suggestions for such an index have been made (see Kokko et al., 1999; Nonacs, 2003, for a review). However, important information may be lost when the variation in reproductive success is expressed as a single value. Crespi and Yanega (1995) pointed out that very different distributions of reproduction can produce the same skew index value, while populations with the same social system could end up with significantly different values if they, for example, differ in patterns of mortality without this being properly accounted for. An alternative way of studying mating systems and sexual selection is to develop theoretical models which may be able to describe the mechanisms involved in producing the observed distributions of reproductive success, and thus retain and explain more information about the systems being studied. In addition to sexual selection, mating system models may be used to study the effect of mating systems on, for example, genetic drift and extinction dynamics.

A number of models representing different aspects of mating systems have been developed. For example, mate choice has been extensively modeled (e.g. Janetos, 1980; Parker, 1983; Hubbell and Johnson, 1987; Real, 1990). Mating rates and mating probabilities have been studied through several different models (Taylor, 1975; Gimelfarb, 1988a, b; Møller and Legendre, 2001; Bessa-Gomes et al., 2003, 2004), all focusing on different contributing factors. The majority of these models are purely deterministic, not allowing for any random events in the mating system. This limits their realism. Different types of mating systems are often modeled separately (e.g. separate models for monogamous populations, populations with a specific harem size, etc.), and some models allow changes in only one mating system characteristic at a time.

The purpose of this paper is to present a general, stochastic model of the pair formation process. This model uses two basic factors, interdependence of mating events and effective equality of male mating probabilities, to describe a continuous range of mating systems from strict monogamy to extreme polygyny. It will be used to investigate how these two mating system characteristics affect the distribution of male mating success and the opportunity for sexual selection in populations with different numbers of males and females.

2. The model

Consider a population of m potentially breeding males and f potentially breeding females. Assume that females mate only once each and that all pair formation/mating takes place at roughly the same time and with no carry-over effects from previous breeding seasons. Fig. 1 gives a schematic overview of how this system is being modeled.

Males in a breeding population will seldom be identical. Differences in phenotypic traits can translate into differences in mating probability, mainly through the influence of male–male competition and female mate choice (Andersson, 1994). In order to model this inequality, each male in the model is assigned a value chosen independently and at random from a gamma distribution with shape parameter k. These values are then scaled by dividing each