Available online at www.sciencedirect.com
ScienceDirect

ELSEVIER

Journal of Theoretical Biology 250 (2008) 524–531

Journal of Theoretical Biology

www.elsevier.com/locate/yjtbi

A model for the evolutionary maintenance of monogyny in spiders

Lutz Fromhage[a,*], John M. McNamara[b], Alasdair I. Houston[a]

[a]*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*
[b]*Department of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, UK*

Received 10 July 2007; received in revised form 8 October 2007; accepted 8 October 2007
Available online 11 October 2007

Abstract

Sexual selection theory predicts that males should attempt to mate with several females, unless the benefits of male promiscuity are trumped by alternative benefits associated with male monogamy (monogyny). Here we use a game theory model to address the adaptive value of a monogynous strategy, which has the sole benefit of enhancing a male's paternity share in the context of competition with other males. We consider two ways in which monogynists might enhance their paternity: by outcompeting rival ejaculates in sperm competition, and by reducing the probability that a female remates with rival males. The model is based on the biology of some particularly well-studied spider species, in which males are morphologically restricted to mate with either one or at most two females in their lifetime. Our results suggest that, regardless of the mechanism of paternity enhancement involved, a male-biased sex ratio is generally required for the evolution and maintenance of monogyny. Moreover, we show that there is a large region of parameter space where monogyny and bigyny can coexist as alternative mating strategies under negative frequency dependent selection. There is also a narrow range of conditions where either monogyny or bigyny can be evolutionarily stable. Our results are in qualitative agreement with empirical findings in spiders.
© 2007 Elsevier Ltd. All rights reserved.

Keywords: Mating strategy; Monogamy; Paternity; Game theory; Sex ratio

---

1. Introduction

Classical sexual selection theory predicts that males should typically maximize their fitness by mating with several females (Bateman, 1948; Trivers, 1972). Exceptions to this rule, however, can evolve in species where the benefits of male promiscuity are trumped by benefits to males that focus their efforts on a single female. The benefits associated with male monogamy (monogyny) can be broadly divided in two classes: first, monogynous males may increase their reproductive success by increasing the number of surviving offspring of their mate. They may achieve this by providing a parental investment (i.e., by supplying the female and/or her offspring with care and resources; Clutton-Brock, 1991; Fromhage et al., 2007b; Trivers, 1972), and by ensuring female fertility through repeated copulations (Wickler and Seibt, 1981). A second possibility, on which we focus in the present study, is that monogynous males may enhance their paternity share in the face of competition by other males. Although parental investment and paternity enhancement are not mutually exclusive activities (Kvarnemo, 2006), a promising approach to studying their significance is to focus on relatively simple systems in which only one of these activities is relevant in the absence of the other.

Here we use a game theory model to address the adaptive value of a monogynous strategy which has the sole benefit of enhancing a male's paternity share in the context of competition with other males. Because such behavior has been described in several particularly well-studied species of spiders (see Andrade and Kasumovic, 2005 for an overview), we couch our model in spider terms. Spider males have paired copulatory organs, the pedipalps. Although females in entelegyne spiders have two separate genital openings, a single pedipalp insertion into one of these openings can fertilize a female's lifetime production of eggs (Andrade and Banta, 2002; Schneider et al., 2005). In several species where

---

*Corresponding author. Tel.: +44 1179545945; fax: +44 1179257374.
E-mail addresses: lutzfromhage@web.de (L. Fromhage), John.McNamara@bristol.ac.uk (J.M. McNamara), A.I.Houston@bristol.ac.uk (A.I. Houston).

0022-5193/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2007.10.008

monogynous mating behavior occurs, the pedipalps regularly become damaged (or depleted of sperm) as a result of copulation, so that each pedipalp can be used for one copulation only (Andrade and Banta, 2002; Foellmer and Fairbairn, 2003; Fromhage and Schneider, 2005b; Herberstein et al., 2005b; but see Breene and Sweet, 1985). Given this constraint, males have only two options: either to use both pedipalps to copulate with the same female (monogyny), or to use each pedipalp to copulate with a different female (bigyny). Although a constraint limiting males to a maximum of two copulations may not necessarily apply in situations where monogyny evolves *de novo* (because this constraint may itself be a consequence of selection for monogyny; cf. Fromhage et al.'s (2005) approach of comparing monogyny with a polygynous strategy of multiple mating), we here take this constraint as given, thus focussing on a comparison between the adaptive value of monogyny versus bigyny. By doing so, we aim to improve the understanding of mating systems in which this constraint currently applies. Another difference between the present study and that of Fromhage et al. (2005) is that we explicitly consider two ways in which monogynists might enhance their paternity: by outcompeting rival ejaculates in sperm competition, and by reducing the probability that a female remates with rival males. In spiders, the latter goal is achieved through mechanisms such as mate-guarding (Christenson and Goist, 1979), self-sacrifice to a cannibalistic female (Andrade, 1996), and mating plugs formed either of broken copulatory organs (Fromhage and Schneider, 2006) or a male's dead body (Foellmer and Fairbairn, 2003). Another possible means of preventing female remating would be the transfer of ejaculate components that manipulate female behavior, as has been documented in insects (Chapman et al., 2003). We take into account that males in web-building spiders are the mate-searching sex, and are hence typically exposed to an increased risk of mortality compared to the sedentary females (Andrade, 2003; Kasumovic et al., 2007; Vollrath and Parker, 1992). Our aim is to address the conditions under which monogyny is likely to evolve and to be maintained by selection.

2. The model

We envisage a large population of constant size, in which a steady influx of newly maturing individuals is offset by a matching rate of death. For simplicity, we assume that all characteristics of the population are stationary in time, i.e., there is no element of seasonality in our model. There are two kinds of males: monogynists, who mate with one female only, and bigynists, who attempt to mate with two females. Males sequentially search for females, attempting to mate with every female they encounter. A male may die either during the search, or after achieving his maximum number of matings. We define m ($0<m<1$) as the mortality risk encountered by a male each time he searches for a female. Implicit in this parameter are all factors that may affect male travel mortality, such as search efficiency and population density. Each female has a fixed lifespan, during which she is available for encounters with males, and at the end of which she lays eggs and dies. Note that because female lifespan is a determinant of female density, it too is implicit in the parameter m. We assume that the probability that a female experiences a mating attempt at any given time is independent of previous attempts that she has experienced; in other words, mating attempts are randomly distributed across females. We further assume that each female is initially receptive when she becomes mature, so that mating attempts with her are successful (i.e., result in mating) with probability 1. Monogynists, however, reduce the probability of remating in their mate, such that further mating attempts with her are successful with a reduced probability y (where $0 \leqslant y \leqslant 1$).

Many quantities used to describe our model are scaled by the number of females. It will be convenient to refer to such relative quantities as if they were absolute quantities. For example, to express the fact that a fraction F of all females experience a given mating history, we might say that there are F such females. Similarly, if there are c mating attempts per female, we might say that there are c attempts.

2.1. Monogynist mating attempts

In this section we derive the number of monogynist mating attempts per female. By definition, monogynists can mate with one female only. Although in spiders this may involve two separate pedipalp insertions, we refer to this as a single mating. Because we have assumed that bigynist mating attempts do not interfere with other (monogynist or bigynist) mating attempts, we can disregard them for the time being and focus exclusively on monogynist attempts. If mating attempts were always successful, the expected number of mating attempts per monogynist would equal $(1-m)$, the probability of surviving until finding a female. Defining p ($0<p<1$) as the proportion of monogynists among all males, and TSR as the tertiary sex ratio of mature males to females that enter the population, there would then be $TSR\,p(1-m)$ monogynist mating attempts per female. The number of attempts will be greater, however, if not all attempts are successful. Let G be the success probability per attempt, i.e., the probability that an attempt results in mating. Then, if a monogynist makes an unsuccessful attempt (with probability $1-G$) and if he survives another search (with probability $1-m$), he will make another attempt. This second attempt may be followed by a third one and so on, until the male is either successful or dies. The resulting number of monogynist mating attempts is given by

$$c_m = \sum_{i=0}^{\infty} TSR\,p(1-m)((1-G)(1-m))^i = \frac{TSR\,p(1-m)}{1-(1-G)(1-m)}. \quad (1)$$

Download English Version:

https://daneshyari.com/en/article/4498724

Download Persian Version:

https://daneshyari.com/article/4498724

Daneshyari.com