

Ecology – Life Histories and the Role of Sexual Reproduction

Sexual Reproduction in Organisms and the Selective Forces Associated with Sex

Reproduction a.k.a. continuity of form

- Here we are getting right at the heart of the measure of fitness, i.e., the passing of genes from one generation to the next
- We can look at this from the perspective of the two general reproductive modes
  - Asexual reproduction is the creation of progeny without contribution from another individual
  - Alternatively, sexual reproduction requires gametes produced by two different individuals (generally through the process of reduction division)

One of the greatest questions…

- Why is there sex?
- The commonly proposed benefit is the production of large amounts of **variability** in subsequent generations and therefore the greater capacity to change. This translates to the *capacity* for more rapid change and adaptation to changing environments
- Similarly, sexual reproduction provides mechanisms to **edit mutations** from offspring with the process of recombination and crossing-over

Correlation to the Environment?

- Historically, we considered the primary factors that created selection pressures for organisms were associated with the physical environment (abiotic)
- **Views of the environments** took center stage with regard to the determination of the frequency of the alternative reproductive modes
  - Asexual reproduction should be most common in predictable, stable conditions (no need to change?)
  - Sexual reproduction should be most common in unpredictable or unstable physical environments

But, the Red Queen Hypothesis

- The predictions of this model suggest that the need for sexual reproduction is a **response to the other organisms** in that particular habitat – you must change as quickly as possible, just to stay even with the predators, parasites and competitors
- The predictions here suggest that when and where **biotic** pressures are greatest, we should see sexual reproduction most common

- “You must run (change) as fast as you can just to stay in the same place” – here we refer to the position of the animals in relation to others in that habitat (i.e. symbioses)

Any support?

- Yes, in fact there is support for this hypothesis
- We often think of sexual reproduction as being an important component in addressing environmental variability, and it is, but sexual reproduction is no less common in stable habitats, *and some evidence even suggests that it is more common*, given the nature of the coevolutionary pressures faced by the species that are in ***a race*** with another evolving species

Mechanisms of Adaptation in a PREDATOR**-**PREY ARMS RACE**: TTX-Resistant Sodium Channels**

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- Populations of the garter snake *Thamnophis sirtalis* have evolved geographically variable resistance to tetrodotoxin (TTX) in a coevolutionary ARMS RACE with their toxic PREY, newts of the genus *Taricha*. Here, we identify a physiological mechanism, the expression of TTX-resistant sodium channels in skeletal muscle, responsible for adaptive diversification in whole-animal resistance. Both individual and population differences in the ability of skeletal muscle fibers to function in the presence of TTX correlate closely with whole-animal measures of TTX resistance. Demonstration of individual variation in an essential physiological function responsible for the adaptive differences among populations is a step toward linking the selective consequences of coevolutionary interactions to geographic and phylogenetic patterns of diversity.

But, there are costs associated with sexual reproduction

- Cost of **sharing the genetic composition** of the offspring – would it not be better to have *all* of your genes in each offspring?
- Cost of **meiosis**, that is breaking up good combinations of genes, from an adaptive standpoint
- Cost of **producing males**. A single male can produce enough sperm to fertilize many females, therefore producing males is a liability
- Finally, the cost of **courtship and mating** – which translates to time and energy costs that could be saved in an asexual mode

Level of Benefits?

- Often sexual reproduction is looked upon as **beneficial to the species** or the population, but this may also be extended to the individual level in addressing the survivorship of your own genes – if your offspring win the race, then your fitness continues to dominate
- And as we noted before this race is not limited to abiotic conditions, it is also the biotic components in the environment that are placing the selective pressures on the populations and the individuals in that population

How do we go about reproducing?

- There is little doubt that reproduction plays a central role in the lives of organisms – sometimes the only role in particular stages of ontogeny
- From an **asexual perspective**, it is rather straight-forward, you either do it by fission, budding or certain types of parthenogenesis
- But this is an individual and generally the mode of asexual reproduction **practiced is based upon the evolutionary history** of the group

Let us look at a type of selection

- Here, we wish to consider the concept of **sexual selection** and its influence on the ability of the individual to mate successfully
- This concept was first addressed by Darwin in terms of the apparent advantage certain individuals have over others of the same sex ***solely with respect to reproduction***
- The result of this process is typically expressed as **sexual dimorphism** and generally with respect to **secondary sexual characteristics**

The implication here?

- Sexual selection produces inter-individual differences associated with mate choice by members of the opposite sex
- The basic concept is that the differential reproductive success is in regard to the number of mates obtained by an individual
- But we can further distinguish *intrasexual* selection and *intersexual* selection

Within or Between?

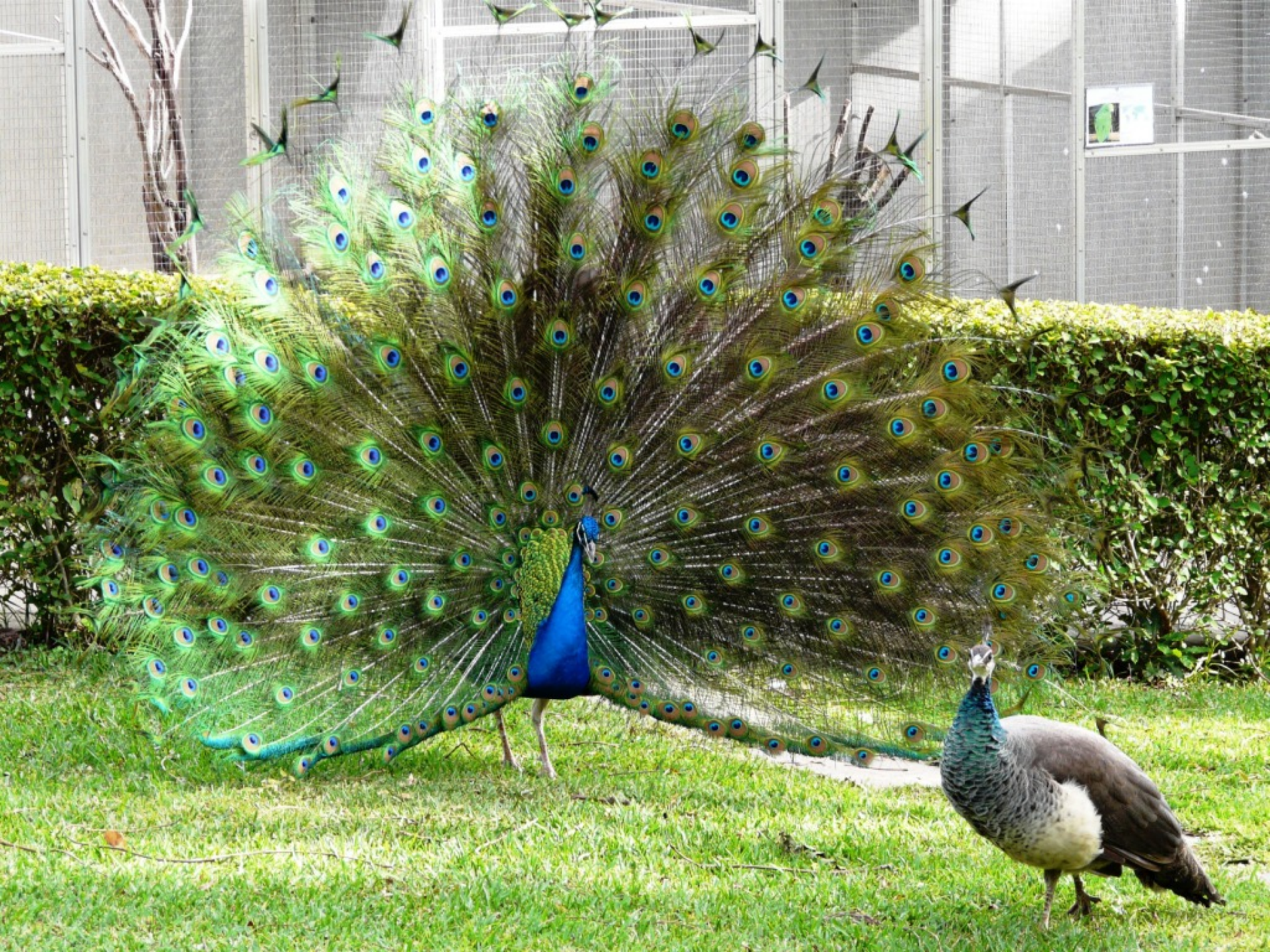
- **Intrasexual** selection is typified by interactions among members of the sex being selected
- Often this is manifested in **competition** and generally centers around **aggressive behavioral patterns**
- When the opposite sex is simply selecting among a group of individuals, this is the situation of intersexual selection

The real difference between males and females

- It has been said that the difference between males and females is a direct function of the **size of the gametes**
- Given that females contribute more to the zygote, i.e. they have a greater investment initially (and often spend more time and parental care), **females generally do the picking** of mates among the group of contending males
- Females are fixed in their reproductive effort regardless of how many times they mate – however, the same is not true for males

But what is the mechanism?

- Sexual selection has been formally recognized as a real phenomenon since Darwin's publication of his work on selection in relation to sex
- There have been several mechanisms proposed in regard to the selective forces associated with change in these species



Fisher's view of Sexual Selection

- As females pick males with more elaborate characteristics, the offspring of such matings produce more individuals with similar characters ***and*** similar preferences
- This creates a positive feedback system such that the intersex selective force continues to drive the mean phenotypic value for that character and create what Fisher has called **"Runaway Selection"**
- The reality check is the balancing of selective forces associated with survival, and not just reproduction

Alternatively,

- A male that sports a unique feature, or an elaboration of a normal feature may be viewed in another light
- The potential negatives associated with this feature are a clear indication of the superior abilities of the individual that has this feature – i.e., this individual must be ***very*** good to survive with this ***"handicap"*** (the handicap principle)
- However, there should be **no asymmetries** in these features. This tends to decrease mating successes

What the female is evaluating…

- We cannot ask most female animals why they are picking a particular mate, and the evidence suggests that the **preference is heritable**, so they could not tell us anyway
- Whether it is a natural selection argument or a sexual selection argument, the end result is basically the same – **strong sexual dimorphism with the high investment sex doing the selecting**

If this is true, then what are the predicted relationships?

- As a general rule of thumb, it is the female that provides a greater investment – that is, in situations where the male does not care for the fertilized eggs or offspring
- And this dimorphism should be extreme, particularly in situations of polygyny
- To fully evaluate this, **we should be able to correlate the investment of care with the level of dimorphism**

Dimorphism and Care

- The **more equal the care, the less the dimorphism**, because both parents are investing heavily in the offspring, and therefore both are picking mates
- What about situations where the male provides disproportionate care for the offspring? It works (generally, but not all of the time)! The dimorphism does not always involve morphological differentiation, it is also behavioral (for example territories or even the number of conflicts)

But it does not stop at care

- Courtship or nuptial feeding is a common mechanism to enhance reproductive success. This works on several levels:
  - This gives the female something to do during copulation
  - The food may be incorporated into the tissues of the female increasing her ability to care for the offspring
  - And some of this food may also be incorporated into the eggs directly (offspring)

This tends to turn the tables

- At least a little…
- When the male is supplying the female with food, **he is investing in those offspring**, above and beyond the gamete
- This nutritional material is not necessarily food, it can be secreted material associated with the sperm and this even creates some competition among females for this source of nutrients

One feature that may accompany dimorphic forms is…

- **Disruptive selection**
- The models are relatively simplistic, but simple is good
- In a population, females (or the picking sex), may exhibit polymorphisms for the morph of choice (intersexual selection). For example, some like short tail feathers and others like long tail feathers
- Differential selection of morphs based upon genetic differences leads to prezygotic isolating mechanisms and potentially speciation
- These models are particularly valuable in the assessment of situations where natural selective forces are reduced

Sexual Behaviors

- One aspect of sexual reproduction is the common occurrence of **aggressive behaviors** and tendencies, but this is not always the case and certainly not with every species
- There are generally periods initially where even clearly opposite sex individuals are chased in aggressive fashions, but this may be communication of other information, rather than exhibition or manifestation of aggressive programs

Neural Mechanisms and Genetics

- The nervous system is working in conjunction with the endocrine system in the production of aggression (at many levels). That we will see in association with the external factors in aggression
- And, we know the foundation of aggression, as with other programs, is passed from generation to generation and subject to natural selection – **it *is* genetic**

Aggression and Sex

- Most of the aggression we see in reproductive activities is associated with competition for territories, access to resources and certainly, access to mates – features that will enhance the reproductive output of an individual
- **Similarly**, observations of the early stages of courtship and even copulation, generally include aggressive components

A balancing act

- This becomes an issue when we look at the activities of organisms in the presence of both potential mates and potential competitors
- The individual is attempting to secure resources – to that end it is openly displaying aggressively to the competitor
- But, at the same time it does not want to frighten the potential mate or mates

Intrasexual Interactions

- The competition for a resource is at the basis for intrasexual selection. It is for the "right" to have access to mates
- What determines the winner of the competition? Generally, this is an issue associated with, or decided by contests
- These contests typically involve weapons, used in a manner such that injuries are minimized **(ritualized interactions)**

What about these selective pressures?

- The competitive nature of these interactions creates **selection for extreme characteristics** (Fisher's runaway selection) and sexual dimorphism
- Any of these features that could potentially be employed in this interaction, that is the contest, can be greatly exaggerated in ways that would seem counter to survival in a natural selection sense

Now what do hippos eat?

Antler size is important

Intersexual Aggressive Interactions

- We talked a bit about this before when we looked at the potential issues facing individuals in the mating process
- Females are typically larger than the males (the whole gamete thing) and **males are often in real danger** by coming close to the females, but sexual reproduction is not a long distance sort of thing, particularly for those forms that require internal fertilization and when there is intrasexual pressures during the fertilization process with external fertilization

Remember Courtship or Nuptial Feeding?

- The males need to find some way to reduce the probability of being eaten by the female, particularly prior to copulation (after the fact would be okay)
- The food enhances the possibility for a successful mating and may ultimately provide extra energy for the female parent and/or the progeny


Black widow

But there is more than being eaten

- There are issues associated with the relationships among the sexes that centers around selfish behaviors and the relationship to conspecifics
- **Individuals will employ strategies that should maximize their individual fitness**
- This behavior is generally at a cost to others in the population and we see adaptations to minimize this sort of impact

The Importance of Reproduction

- There is little doubt that reproduction plays a central role in the lives of organisms – after all, if an individual is unable to reproduce, we have some serious fitness issues
- We will now look at two aspects. First we will consider the variation in reproductive strategies (mostly sexually)
- Secondly, often reproducing is not enough, we want to insure the survival of the progeny produced, i.e., investment of parental care

Where to begin…

- In a standard sense, at least for plants, individuals may have both male and female reproductive structures – **hermaphrodites** (also known as **monoecious** with separate sex flowers on a single plant or *perfect* if each flower contains both male and female reproductive structures in botanical circles)
- For animals the standard is somewhat different – **gonochorism** or **dioecious** organisms are separate male and female individuals

But, plants are not alone

- That is, many animals are also hermaphroditic, maintaining both male and female reproductive structures in a single individual
- There is a great amount of variation in the different kinds of activities we see in these forms – most of which is based upon the timing of the maturity of the gonads
- Name some of the groups?

Under what conditions might hermaphroditism be favored?

- Think about this from a functional perspective for the reproductive effort, why might it be beneficial to be a hermaphrodite?
- What types of environments?

Another *unusual* system

- In many hymenopteran species, we find a system where males are derived from haploid eggs and females from fertilized diploid eggs – haplodiploidy
- This system is controlled by the female as she lays her eggs. If sperm is not released, the eggs develop parthenogenetically into haploid males. If sperm is released the eggs are fertilized and the resulting offspring are all diploid females

Theory of Mating Systems

- The theoretical foundation for mating systems corresponds to the basic asymmetry of reproduction – the success of a female is limited by her ability to make eggs and provide for her offspring whereas the success of the male is usually limited by the number of matings he can procure
- It is a *simple* relationship based upon the nature of the gametes in males and females. It is more expensive to produce an egg and, in reality, sperm is cheap

But, is it really *that* simple?

- Of course not, because the young that are produced **must survive to reproductive age** or you have not added to your fitness
- Mating systems vary from **promiscuity to monogamy**, and generally this is viewed from the male's perspective, given the differences associated with gametic contributions
- Promiscuity is the contribution of nothing more than genes and is the most common system in the animals

Mating systems depend to a large degree on the habitat and life history

- Remember the bottom line, it is maximizing the survivorship of the offspring
- If the young require care, i.e. **altricial** young, and a single parent cannot provide for the clutch, it is advantageous to be **monogamous**, or sometimes **even polyandry** develops in these systems

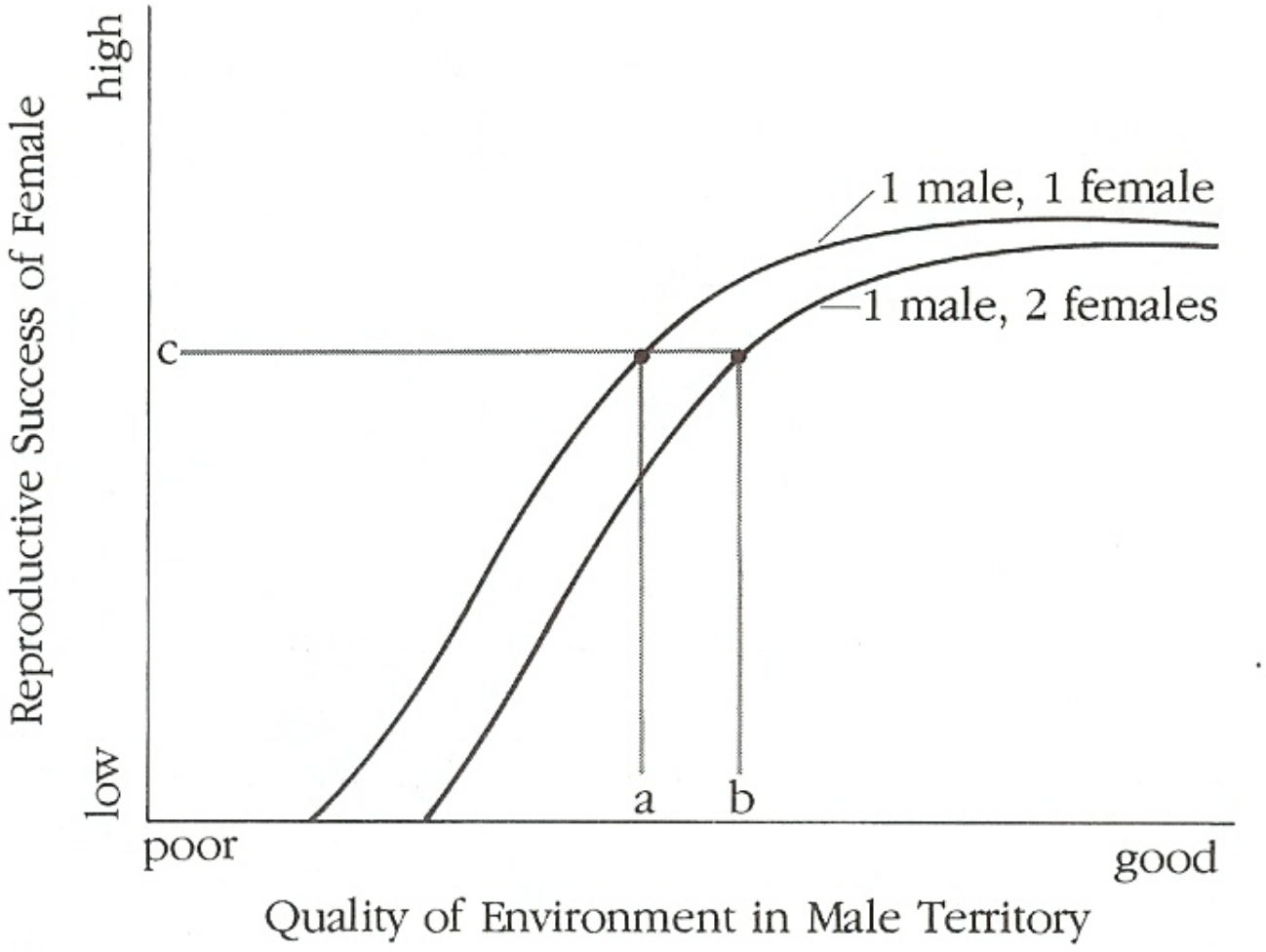
Alternatively, with precocial young

- These situations tend toward promiscuity, or at the very least **polygyny**
- Another feature that contributes to the type of mating system is ***certainty of paternity***
- The female is rather certain about which eggs are hers, but in organisms that practice internal fertilization, where mating and birth are separated temporally, this certainty is much lower for the male. This is thought to be a contributing factor to the **rarity of exclusive male care of offspring in birds and mammals**

Feeding the offspring

- It is not just the matter of altricial and precocial offspring, it is the ability to acquire sufficient resources to support the offspring
- Social system aside, if a mate maintains a territory that is rich in resources, polygyny may be better than monogamy with a lesser quality territory

The Polygyny Threshold



Parental Care

- Parental investment is expensive, in time and energy
- On a very basic level, it is rather important that a parent be able to identify their own offspring and differentiate these individuals from other offspring
- However, at some point in time (when the costs are greater than the benefits) the parent(s) should stop caring for the young

Parent-Offspring Conflict

- There appears to be two sides to this story
  - The parent must at some point cease giving care because of the cost to the individual's reproductive output (i.e. the parent)
  - On the other hand, the offspring should try to gain as much care as possible, to maximize *their* individual fitness – thus the conflict in a fitness sort of light
- This can lead to differential survival of the offspring and even competition among the offspring, where some win and some do not

At the extreme

- This **sibling rivalry** can take on extreme measures when there is not only competition for the attention of a parent, but also competition for limited resources
- Siblicide may result from this type of interaction among individuals in a clutch
- The result is often functional for the parent due to the nature of the conflict – limitations in resources do not allow sufficient supplies for all of the offspring, therefore the one that wins must also be the strongest – still a **win/win**?

What about the parents?

- Well, if siblicide does mean that the one, single best offspring will survive, perhaps this is selectively advantageous
- But, it would be **ideal** to produce lots of offspring *and* have them survive – or at least give them a fighting chance
- We see something called **brood parasitism** in many birds, and particularly among waterfowl

Costs and Benefits

- The potential rewards **and costs** are immense
- The reward to the female is a + 0.5 if successful, but the potential costs include the rearing of some other individual's offspring (- 0.5) and loss of your eggs that you dumped into some other nest
- In fact, when this becomes very common, the individual being parasitized leaves the nest and all of the offspring perish

Data from a study on Wood Ducks

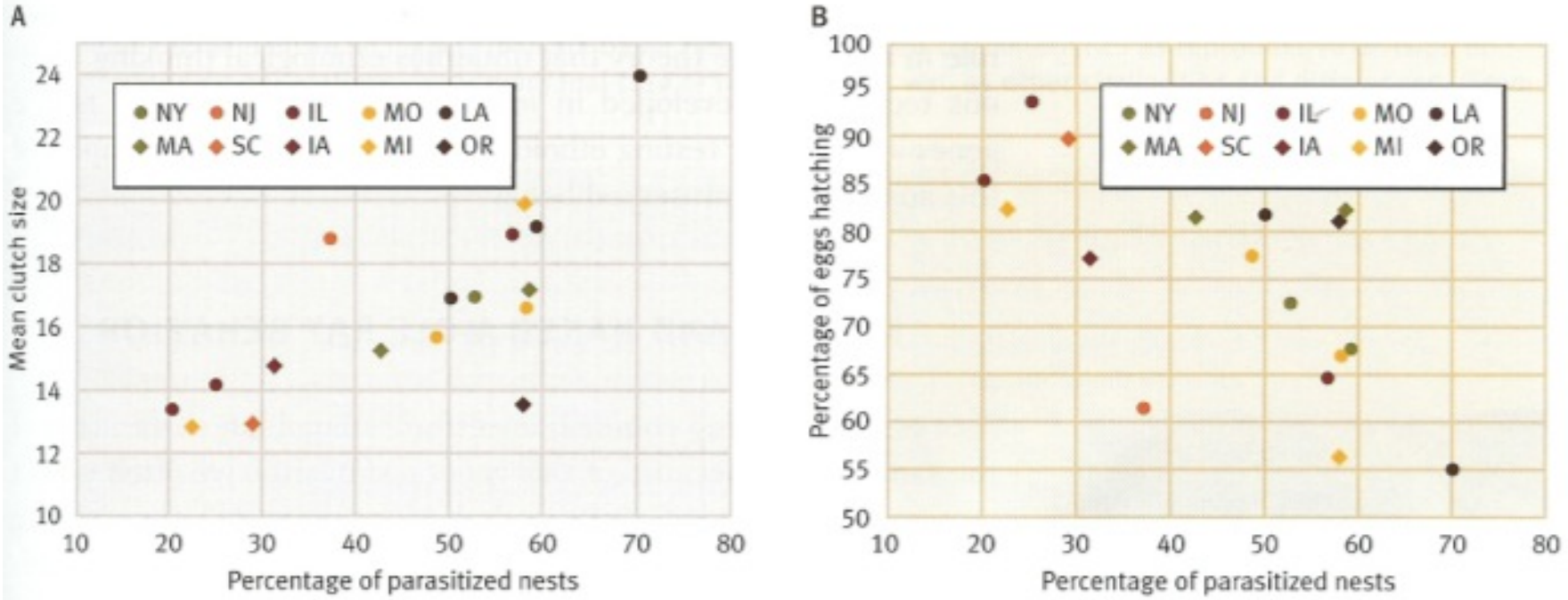


FIGURE 2.24. **Egg dumping and rearing young.** In wood ducks, the level of nest parasitism affects both the number

Population Dynamics

- There appears to be a balance – some parasitism works, but if the whole population engages in this behavior, everyone suffers a lowered reproductive success and we see fluctuations in density

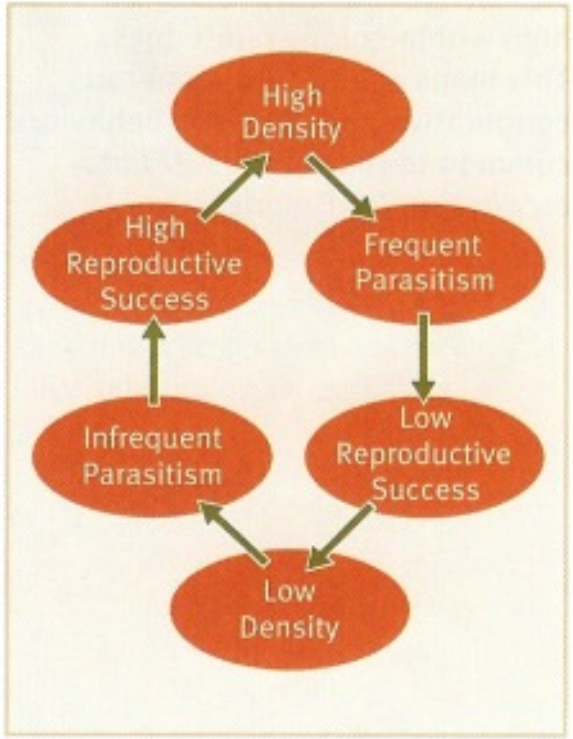


FIGURE 2.25. Population dynamics and nest parasitism. Sherman and Semel argue that both nest parasitism and population density cycle together. *(From Sherman, 2001)*