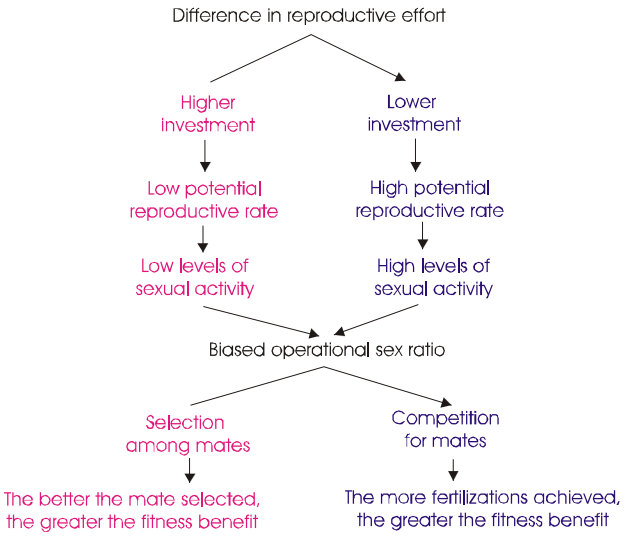
With this chapter we begin a “unit” on reproductive behavior. We’ll start with an exploration of how and why male and female reproductive strategies seem to differ in predictable ways, then follow with discussions of variation in mating systems and parental care. The main points from this chapter are:

1. Differences in male and female reproductive behavior stem from general differences in reproductive potential.
2. Differences in reproductive potential set the stage for sexual selection, an important mechanism of evolution when variation in reproductive success is associated with
   a. intrasexual competition for mates and/or
   b. preferences in one sex for mates with specific attributes (mate choice)
3. Interactions between the sexes involve a combination of “cooperation” and “conflict”, with males generally “acting to” maximize the number of fertilizations and females “acting to” set the rules of mate choice. These differences also help us understand individual male and female strategies of competition and mate choice.
4. In some species, selection has favored male strategies that circumvent female choice, leading to harrassment, forced copulation, and infanticide.

CHAPTER 12: MALE AND FEMALE REPRODUCTIVE TACTICS

A. Differences between sexes in reproductive behavior stem from differences in reproductive potential
   1. General pattern in most species includes combination of
      a. male-male competition,
      b. male courtship of females
      c. female choosiness.

2. Differences arise from differences in parental investment in offspring – which lead, in turn, to differences in the operational sex ratio and, from there, to differences in the kinds of mating strategies favored by selection:



   a. Generally, female reproductive effort > males:
      i. cost of gametes, by definition
      ii. often also differences in parental care
      iii. some differences in cost of gametes, parental care compensated by male nuptial gifts, other benefits (as we'll see later)
   b. Individuals with higher reproductive effort have less time/energy for sexual activity, changing the **operational sex ratio** = proportion of sexually receptive males to females – usually male biased
   c. If operational sex ratio is biased, then selection will favor
      i. competition for mates in the "more abundant" sex – because there are relatively more of them (for mating purposes)
      ii. selectivity in the "less abundant" sex to maximize reproductive benefit relative to the cost (investment) in reproduction

3. This general hypothesis can be tested by looking at examples of "sex role reversal" = exceptions to the usual pattern
    a. prediction = sex role reversal happens when male investment > females
    b. prediction is met in several species:
        i. pipefish:
            a) males brood eggs, provide nutrients & oxygen
            b) females provide eggs only
            c) males prefer larger, more ornamented females (large body size usually indicates large numbers of eggs)
            d) females compete for mates
        ii. Mormon crickets:
            a) males provide large, nutritious spermatophores
            b) females compete for mates
            c) males prefer largest females
        iii. Australian katydids offer strong support, because sex role reversal is itself reversible:
            a) when food resources scarce
                (i) male spermatophores = relatively large investment (male reproductive potential is limited)
                (ii) females compete for males, males selective
            b) when food resources are more abundant
                (i) male spermatophores = relatively small investment
                (ii) males compete for females, females selective
4. Selectively beneficial differences in reproductive strategy set the stage for **sexual selection**
    a. phrase (and process) developed by Darwin to solve "original Darwinian puzzle" of apparently maladaptive male traits like heavy ornamentation
    b. Def: process favoring traits that enhance reproductive success

c. Sexual selection is just a special case of natural selection –
   i. often, natural and sexual selection will favor the same traits (e.g., large body size)
   ii. most investigators find it's most interesting when sexual selection favors traits that "should be" selected against by natural selection (i.e., male ornamentation, making males more vulnerable to predation)

d. In general, sexual selection will
   i. act most strongly in the "more abundant sex" (generally males)
   ii. favor traits that enhance
      a) competitive ability in contests with other males
      b) attractiveness to females

B. Patterns and processes of male-male competition

1. Direct competition for dominance

a. probably most common form, and most obvious

b. involves direct interactions among males such that winner has greatest access to reproductive females
   i. access can be direct – e.g., dominant male baboons have most access to fertile females
   ii. access can be indirect, as when dominant male gets best territories, which are actually the objects of female choice

c. in this case, selection favors traits that enhance "combat" ability:
   i. large body size
   ii. "weapons" = horns, antlers, etc.

d. interestingly, degree of sexual dimorphism (difference in body size between males and females) is often a good indicator of the degree of polygyny in that species: the greater the bias in the operational sex ratio, the greater the degree of polygyny and the greater the benefit that will accrue to the largest males (what does this imply about humans?)

2. In many species with direct competition for dominance, actually find multiple mating tactics among males
   a. e.g., satellite males = nonagressive individuals that "hang out" near more aggressive, dominant males
   b. two mechanisms can account for different mating strategies within a single species:
      i. "**separate strategies**" = tactics provide equal fitness benefits and are inherited (i.e., differences in tactics are caused by genetic differences among males)
      ii. "**conditional strategy**" = tactics provide unequal fitness benefits; males adopt the tactic that provides maximum benefits under specific environmental conditions
   c. Example of separate strategies: sponge isopod
      i. 3 "types" of males based on body size (alpha, beta, gamma)
      ii. in single encounters in cavities in sponges:
         a) alphas physically remove gammas from cavities
         b) betas meeting alphas mimic females, so alphas permit coexistence
      iii. Shuster and colleagues found that
         a) size and behavioral differences stemmed largely from genetic differences among individuals
         b) in natural environment, no significant difference in reproductive success (measured by numbers of females mated) among the three types
         c) consistent with separate strategy hypothesis
   d. Example of conditional strategy = <u>Panorpa</u> scorpionflies
      i. 3 male types based on mate acquisiton tactics:
         a) Type I: drive others away from dead insects, which attract females
         b) Type II: provide salivary secretions as nuptial gifts for females

c) Type III: attempt to force copulation

ii. Thornhill found that

a) differences in strategy were correlated with both male body size and reproductive success – so fitness benefits not equal

b) when largest (Type I) males removed from experimental enclosures, got changes in tactics of the other two:

(i) Type II abandoned secretions and started defending prey (crickets)

(ii) Type III took over the secretions of the Type II

c) supports the conditional strategy hypothesis

e. as a general rule, most examples that have been carefully studied have turned out to be conditional strategies – these seem to be more common

3. Sperm competition is a form of male-male competition often found when females mate with multiple males

a. involves any strategy by which an individual male increases the likelihood that his sperm fertilize the most eggs

b. e.g., male insects sometimes have intromittent organs modified as “sperm scrubbers” that remove previous male’s sperm before depositing own

c. another potential mechanism is increased frequency of copulation (possibly in conjunction with mate-guarding)

4. Mate guarding is a form of male-male competition that increases the likelihood that no other male will inseminate mate prior to fertilization

a. can take a direct form, in which males aggressively defend females from rival males (or prevent females from leaving)

b. can take the indirect form of copulatory plugs = secretions that plug up female reproductive tract, preventing another male from inseminating her

c. note that mate guarding carries potential cost: a male guarding a female cannot himself be seeking additional copulations; in general

i. benefits of guarding increase with probability that unguarded female will

mate again

ii. costs decrease with availability of receptive females

iii. read about Idaho and Belding's ground squirrels (p. 454) – which will practice mate guarding?

C. Faced with a choice among competing males, females can use a variety of traits as the basis for selecting mates (see Table 2)

1. Material benefits: female chooses male that provides material benefits that increase her reproductive success

a. **nuptial gifts** = food resources

i. may provide direct benefit in the form of calories, nutrients, or other constituents (ions, protective chemicals) allocated directly to eggs

ii. may provide indirect benefit in the form of resources for female's own maintenance

b. services, often protection

i. e.g., against predators (white-tailed ptarmigan)

ii. e.g., protection of female's other offspring (baboons)

c. territorial resources: females select best territories, mating with territory owners – territories may be "judged" based on

i. availability of food

ii. suitability of nest sites

iii. degree of predation risk

2. Appearance and courtship: females choose males based on their degree of ornamentation (females select "flashiest" male)

a. here, **ornamentation** = any kind of sensory stimulus – may be visible, acoustic, chemical, tactile

b. in these cases, the proximate mechanism of choice is the degree of sensory stimulation of female – but what is the ultimate mechanism? I.e., what do females gain by mating with most ornamented male?

c. several mechanisms are possible – note I organize these a bit differently than Alcock does
   i. in species with direct investment by males, the degree of ornamentation may be a **reliable signal of the degree of male investment** – so females are using ornamentation as a measure of material benefit
      a) e.g., female pied flycatchers prefer males with black and white feathers
      b) those males are also the best at providing food for young
   ii. in species with no direct investment by males, two possibilities:
      a) **good genes**: male ornamentation is a reliable indicator of some measure of genetic quality – traits that will enhance the fitness of the female's offspring. Several different ways this can work:
         (i) **parasite load**: in several bird species and in crickets, degree of ornamentation is lower in males with most parasites – females benefit from either (or both)
            1) lower risk of contagion
            2) improved resistance
         (ii) **developmental homeostasis**: females prefer most bilaterally symmetric males; hypothesis is that symmetry is a good measure of resistance to "developmental accidents"
         (iii) **handicap principle**: most ornamented males are the most handicapped; must have excellent underlying physiological systems etc. to survive
            1) assumes that ornaments require substantial energy to build and maintain
            2) males that manage to survive with best ornaments must have
               a) best underlying physiological systems
               b) best ability to acquire food resources

c) best ability to avoid predation

b) **runaway selection**: female choice is largely "accidental", ultimately favored by selection because choosiest females have "sexy sons"

(i) in theory, runaway sexual selection can produce ornamentation whenever

1) genetic variation exists for both female preference and male ornament

2) selectiveness provides even slight advantage to females

(ii) thought experiment: hypothetical species of bird has variation in male feather color, variation in female preference:

1) most males drab, some have reddish feathers

2) most females not choosy, some prefer red-feathered males (and get slight fitness advantage)

3) selection will favor choosy females:

a) initially because of slight fitness advantage

b) as frequency of choosy females increases, selection will favor choosiness because choosy females have the most ornamented sons – and they'll be more likely to mate than drab ones

4) selection will favor most ornamented males as they're the ones most attractive to choosy females

(iii) result can be that fitness benefits of ornamentation/selectivity outweigh whatever initial benefits were; selection "runs away" with the process, producing every-choosier females and increasingly ornamented males

(iv) process stops when other fitness costs of ornamentation outweigh its benefits for female choice

(v) we may find that sensory exploitation alone can get the process started – even without a slight fitness advantage to choice!

d. Distinguishing which mechanism is operating in any one case may be difficult, at least in part because they're not mutually exclusive. However,
   i. in general, good genes models predict direct correlation between male ornamentation and some performance advantage in offpsring
   ii. parasite load hypothesis predictions fairly straight-forward:
      a) should see negative correlation between male ornamentation and male parasite load
      b) should see negative correlation between male ornamentation and offspring parasite load
   iii. runaway hypothesis predicts no relationship between performance advantage (other than attractiveness) and male ornamentation, so can be excluded if such a relationship found (e.g., peacocks, cockroaches)

3. Sexual suicide: males offer themselves as nuptial gifts to females
   a. probably fairly rare, in spite of occurrence of sexual cannabilism (i.e., sexual cannabilism probably primarily a matter of bad luck on the part of males)
   b. read example of red-back spiders
4. Female choice may be cryptic: females may choose among sperm after copulation, rather than among males before copulation
   a. if this is the case, expect to see male behaviors that increase the likelihood that their sperm is chosen (see sperm competition above)

D. In many instances, male and female "interests" coincide – males "cooperate" with females to influence mate choice. Sometimes, though, selection favors male traits that allow them to circumvent female choice. Briefly, these include
   1. "Harrassment"/forced copulation: males persist in "courting" females in spite of female behavior indicating unwillingness; this may result in
   2. Induced abortion: previously-mated females abort/resorb embryos when mate

replaced; male can then inseminate females

3. Infanticide: males acquiring mates kill previous offspring so parental investment (male and female) directed at own offspring