Chapter 10 -- Sexual Ornaments and Mate Choice

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Mate Choice and Sexual Ornaments

Why do Females Choose and Males Display?

Get out of your chair and go look at some animals behaving. I hope that spring is in the air so that you can see animals courting and mating. Look at insects, birds, mammals, or reptiles. Go to the beach and look at the fiddler crabs. So sad if the dead of winter has set in and animals aren't engaged in mating rituals. Look at fish in an aquarium. Go to a tropical fish store and look at a tank of guppies. If no animals are about, or you just feel like being an armchair behaviorist, reach into your memories. Failing the easy availability of wild animals or leaky memory banks, look at humans. Go to places where people like to see and be seen. When you analyze your observations of mating behaviors, you will find that males tend to strut, while females watch. The basis of this simple observation, leads to a powerful theorem of sexual selection. Females tend to be the choosier sex while males tend to display to females. Why is it that females do the choosing in most animals?

The observation that males strut and females choose is not universally true. Females often display back. As we will find out, these exceptions to the rule really only prove the rule. So let us rephrase our theorem of sexual selection. The sex that invests more heavily in reproduction will tend to be the choosier sex, while the other sex will tend to display and develop ornaments to enhance their attractiveness.

In the previous chapter, we found that one sex will be selected to produce small gametes. Microgametes, or sperm, are selected for their ability to find the macrogametes, or eggs. The egg is selected for its nutritive capabilities -- for nourishing the newly fertilized zygote. In the long run, the sex with small gametes will end up investing far less energy in reproduction than the other sex that is selected to produce large gametes. Because females of most species end up expending more energy in reproduction than males, males are often free to solicit additional mating opportunities with other females. Females labor under the burden of their investment. This creates a surplus of males on the market. When it comes time for a female to reproduce, the surplus of males gives her the advantages of choice (Trivers 1972).

The role of female choice in promoting sexual selection is largely tied to

the observation that females invest more heavily in reproduction, making them a limiting resource. A female that is taking care of young or gathering energy to provision eggs is not interested in mate choice after she copulates with the male. Higher parental investment by females was cited by Trivers (1972) as the primary force that drives sexual selection on elaborate male traits that females use to choose. Whereas the females may invest in acquiring energy for costly eggs, or in prolonged care in young, the male is free to move on and mate with other females, or compete with other males for access to females. Thus, females can be quite choosy about their mate because males are present in abundance. As we shall see later in this chapter, the role of parental investment in mate choice has been powerfully tested in animals with **sex-role reversal**. In sex-role reversed species the male provides parental care (Vincent et al. 1992). In such species, females develop ornaments and display, and males tend to choose. There is also a middle ground to male-female choice, and males and females who share the role of parenting show a more equitable set of displays, and courtship and bonding rituals (see Chapter 11).

Given the bias in availability of males in most animals, females get to choose who they mate with. Therefore, males need a successful ad campaign. It's a classic case of consumer demand in the market place for high quality products. Even if a product is not necessarily of the highest quality, a product will sell quite well if clever packaging is used to entice the consumer. Consumers are constantly bombarded with packaging that makes a product seem more attractive, larger, brighter and more exciting.

The issues of female choice and male ornamentation are entirely analogous to advertising and packaging. Is the flashy packaging an honest representation of the product inside the package? Alternatively, is the advertising industry exploiting our sensory systems? Are we, as consumers, simply attracted to certain colors? Do we tend to gravitate toward packages that stimulate our senses? You may have heard of the days when the advertising industry toyed around with the idea of using **subliminal messages** encoded into television programming. The subliminal advertisements were only designed to last a split second -- so fast that the viewer would not even perceive that they saw a flash of a sumptuous dessert. Nevertheless, after watching the subliminal message,

the viewer would get the overpowering urge to find something sweet to eat. Thankfully, the days of subliminal messages on television never really materialized. The idea of a perceptual bias in evolution is very much analogous to the process that subliminal messages try to tap. Evolution may have crafted males to become either honest advertisements of quality, or alternatively, stimulating advertisements that excite and entice. But deep down, are these messages honest?

Figure 10.1. Variation in ornaments among male and female species of birds of paradise (top - *Diphyllodes respublica*, middle - *Lophorina superba*, bottom - *Seleucidis melanoleuca*). Whereas males (left) are greatly varied in the ornaments that adorn their bodies, females (right) are very uniform among species. Males have bizarre ornaments that seem to serve no other function besides mate attraction. (birds from Jägerskiöld, 1908, after (Andersson 1994).

The notion of an advertisement is typified by the ornaments that adorn species in the family Paradisaeidea, the birds of paradise. From the beginning of evolutionary thought, the role or adaptive value of ornamentation, such as those found in birds of paradise, has been a contentious issue. Drawing upon his explorations of the Malay Archipelago where the birds of paradise evolved, Alfred Russell Wallace believed that sexual ornaments in all species were primarily for species recognition (Andersson 1994). However, Charles Darwin (1871) believed that ornaments enhanced the mating success of the adorned males. Modern theories regarding the origin of sexual ornaments appear to support Darwin but remember the examples in Chapter 5 on speciation. The processes by which ornaments are favored by sexual selection remain an unresolved area of Evolutionary Biology. Two different camps have emerged: those that favor a purely attractive value to the ornaments, and those that contend that the ornaments are used by females as indicators of a male's quality. Remember also that ornaments can also be used during male-male competition as badges of status.

Of course, the ornament need not be only be a visual cue, but can be olfactory, chemosensory, auditory, tactile, or even electromagnetic depending on what senses the animal uses for mate choice. In this chapter, I will focus on visual ornaments, but other sensory modalities are explored in upcoming chapters. This is largely because of my primate bias for visual stimuli. New research on humans indicates that we have senses that we never really appreciated, the volmeral-nasal organ, which picks up pheromones from potential partners. Many of the choices that animals make are not necessarily conscious as the example on human pheromones illustrates. Choice is used euphemistically to indicate a non-random association for one mate over another because of some attribute of the phenotype such ornament size or quality. It need not imply active cognition. Surprisingly, there has been very little work on the cognitive aspects of choice, and yet our own experience would suggest that at times we think about who we would want as a future (or current) mate. Isn't it likely that other animals think about such decisions? Alternatively, it may be so important (from the view point of selection) that maybe we shouldn't think about it too much.

Before we enter the modern debate regarding origin and maintenance of female choice and male ornaments, let's consider the evidence for choice tending to rest with females in the animal kingdom. We will consider some interesting exceptions to this generalization -- exceptions that are illuminating in that they demonstrate the key differences between the sexes of most species promote choosy females and males that display and compete for the female's attention. We will then explore the alternative idea that the ornaments used as a form of honest advertisement regarding male quality.

Operational Sex Ratio and Male Care in Fish

Most fish have no parental care, and simply squirt gametes into the water leaving zygotes to develop on their own. This reproductive mode was present in one of the first organisms that we would have called a fish. We refer to this original condition as an **ancestral state** (Brooks and McLennan 1991). **Derived states** would be modifications of the ancestral state that entail evolution of new adaptations. For example, sticklebacks, pipefish, and seahorses belong to the same order of fish, Gasterosteiformes, and are noteworthy in animals for evolving advanced systems of male care. Care from a male parent is derived relative to the ancestral mode of 'broadcast spawning' found in most fish.

The care in sticklebacks is limited to nest defense, a relatively common occurrence in the animal kingdom (e.g., many families of fish, birds, mammals, insects, etc. have males that guard the nest). Some species of male pipefish, *Nerophis ophiodon*, develop a **brood patch** to which eggs are glued, and the male carries the eggs until they hatch. Other species of male pipefish, *Sygnathus typhle*, have developed an elaborate **brood pouch** during the reproductive season, into which the female oviposits her eggs. The pouch splits open when the eggs hatch, releasing the newly developed fry. Male seahorses have evolved elaborate vascularization in the pouch where nutrients are transferred to the eggs much like a female mammal transfers micronutrients across the placenta. The sticklebacks, pipefish and seahorses have a family tree of sorts, a **phylogenetic tree** that describes the order in which each species split off during evolution (Brooks and McLennan 1991). Sticklebacks split off earlier and also have the least derived level of male care in which a nest is defended. Pipefish like *Nerophis ophiodon* that possess a brood patch split off later, while pipefish with a more derived brood pouch, *Syngnathus typle*, split off later. Seahorses with a brood pouch

that completely encases the embryos, the most derived state, split off last. The phylogenetic history for the Gasterosteiformes shows a clear evolutionary progression for more derived traits that enhance male care.
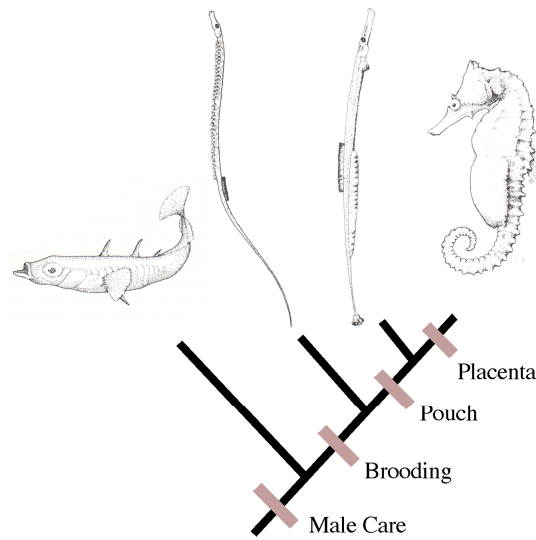

Figure 10.2. A simplified phylogeny for fish in the order Gasterosteiformes illustrating the more derived care that has evolved in more recently evolved pipefish relative to sticklebacks (a more complete phylogeny is given in Chapter 18). Male care in a nest is a derived condition relative to the more ancestral condition of all fish that broadcast spawn gametes (not shown). A simple brood patch is found in pipefish *Nerophis ophiodon*, brood pouch with folds in pipefish *Syngnathus typhle*, and an enclosed pouch in the seahorse, *Hippocampus whitei*. (stickleback from (Drickamer and Vessey 1986), other fish drawings from Vincent et al 1992).

Most fish provide no parental care. In such species, the male is typically the most brightly colored of the sexes. Even in fish where the male cares for the eggs in a nest, males still appear to be the most brightly colored of the sexes (e.g., see the discussion of Hermaphroditic reef fish, and bluegill sunfish, Chapter 9). At first glance, the investment that parental males make in reproduction would suggest that they should be the choosier sex. For example, stickleback males spend several weeks fanning the eggs on a minute-by-minute basis when they are not chasing predators off their territory. This may limit the overall reproductive rate of males compared to females. However, a single stickleback male can readily attract many females to his nest, get them to oviposit one after the other, and then take care of the entire mixed brood of eggs oviposited by several females.
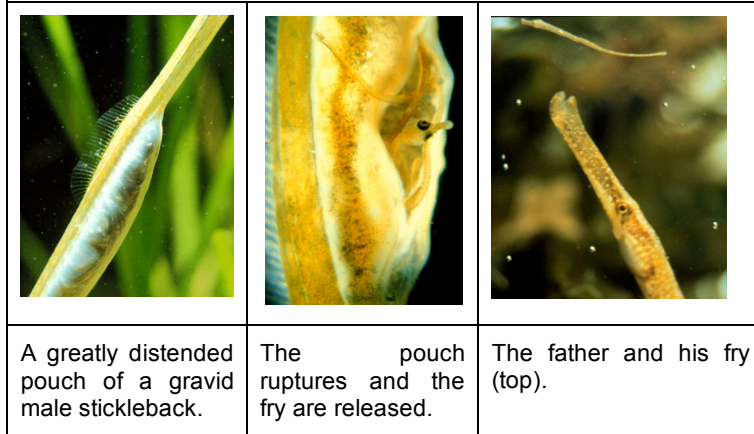
The female stickleback must go in search of additional food to build up enough fat reserves so that she is able to yolk up another clutch of eggs. In sticklebacks, females are still limiting because the process of egg production takes time. Female sticklebacks choose males on the basis of the bright red color on the male belly. The female may be choosing the male for an ornament *per se*, or the orange might actually be an index of the male's quality as a caregiver. Presumably a more vigorous and aggressive male would be better able to ward off other fish that would raid the nest. The female may be searching for such clues about the male's quality. The intensity of the red male's color may indicate the quality of food that he has been feeding on, and hence the quality of food on his territory. The males also use a fanning display, directed to the female, which involves the same pectoral fins that he uses in fanning and aerating eggs. Males with more red or a higher fanning rate are favored by sexual selection (Bakker 1993).

The occurrence of male parental care in sticklebacks would appear to invalidate the hypothesis that ornaments of attraction are expected in the sex with the lowest parental investment. The key point in the arguments by Trivers (1972) is that investment leads to a limited availability of males. Are stickleback males more limiting by virtue of the care that they provide to their young? To decide who has the greater parental investment you need to carefully study the animal's behavior, and the energy they invest in rearing young to determine whether males or females are less available during the breeding season.

The conditions for the evolution of male choice are not met in sticklebacks. Males are not the sex that limits reproductive rate. Female egg production is still a more severe limitation on the production of eggs. Many females are in the process of yolking up eggs, whereas many nest guarding males are still available to fertilize a female's clutch of eggs.

Even though there are equal numbers of males and females, the sex ratio favors the more limited females because there are more males from which to choose -- the operational sex ratio is male-biased. The idea of **operational sex ratio** (Emlen and Oring 1977) explains why male sticklebacks are under strong sexual selection and females still choose males on the basis of their bright red coloration.

Figure 10.3 Stages in the reproductive cycle of the male pipefish, *Sygnathus typhle*. (photos courtesy of A. Berglund).

| A greatly distended pouch of a gravid male stickleback. | The pouch ruptures and the fry are released. | The father and his fry (top). |

Pipefish have evolved a higher level of male care -- a brood pouch (Fig. 10.3). Early in the season, there are many males available, but only for a short time, and females scramble to visit as many males as they can. Males take twice as long to hatch the eggs in their pouch compared to the time it takes for a female to yolk up another clutch. The pipefish *S. typhle* lives in the cool waters of the Gulf of Bothnia, and their breeding season is short. This leads to local mate competition among females to gain access to males. Larger and more heavily ornamented females are usually the victors in this competition. The population has an excess of females that can potentially mate, or the operational sex ratio in pipefish is strongly female-biased, which is a primary requirement for sexual selection to produce female ornaments and male mate choice.

Because of the over-abundance of female pipefish, the size of the male's brood pouch is a limiting resource in pipefish. A male pipefish's pouch only has space for a limited number of embryos. Perhaps he should be quite choosy about the quality of the female. Once a male stickleback is filled up with a load of eggs, female pipefish find him unattractive. Even when a male pipefish's pouch is half-full females find him less attractive. A female with a full load of eggs wants to deposit them in a single mating with a male that has an empty pouch. Both males and females should prefer large mates.

Anders Berglund (1986) tested the choosiness of males and females by offering each male and female *Syngnathus typhle* the choice of different-sized mates. Both sexes chose larger mates. In *S. typhle*, females tend to be larger than males -- they exhibit **reverse sexual dimorphism** over the usual pattern of males being larger than females. In most sexually dimorphic animals males tend to be the larger sex because males compete with other males for access to females (see Chapter 8). Is the larger body size of females driven by male choice or female contest? Female *S. typhle* also use ornaments in contests. Females become greatly darkened during contests and the ornaments turn on when females are engaged in 'shoving matches' with other females over males. Even though the role of female body size and the subtle ornament in females is not entirely clear, females appear to be under stronger sexual selection in *Syngnathus typhle* compared to most other fish. However, both sexes can benefit from choosing large mates in *S. typhle*.

Figure 10.4. (Top) Mate choice for large size is found in both sexes in the pipefish, *Syngnathus typhle*, as both sexes can gain from mating as large an individual as possible. Anders Berglund gave male pipefish a choice of two females in A) open tanks where females could compete, or B) in tanks with a divider. C) Females were given a choice of male in tanks with a divider (from Berglund et al. 1986). (Bottom) Males prefer large female and large female ornaments in the pipefish, *Nerophis ophiodon* (Rosenqvist 1990).
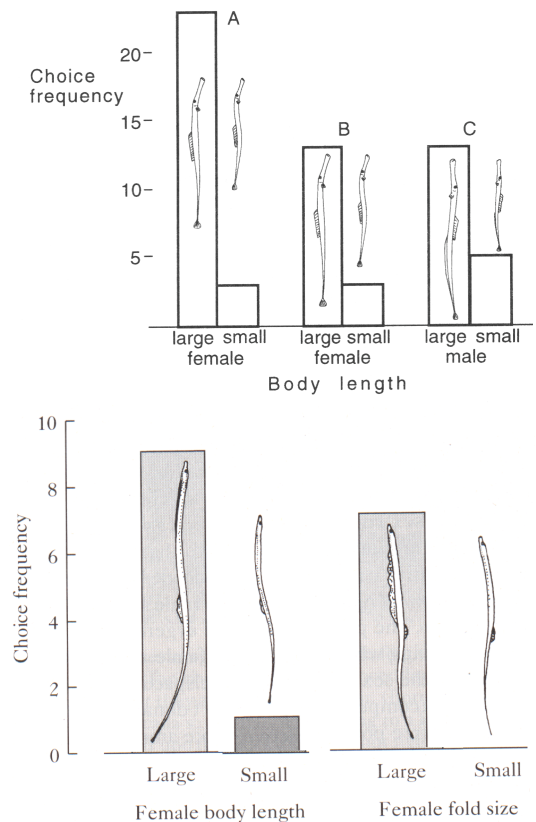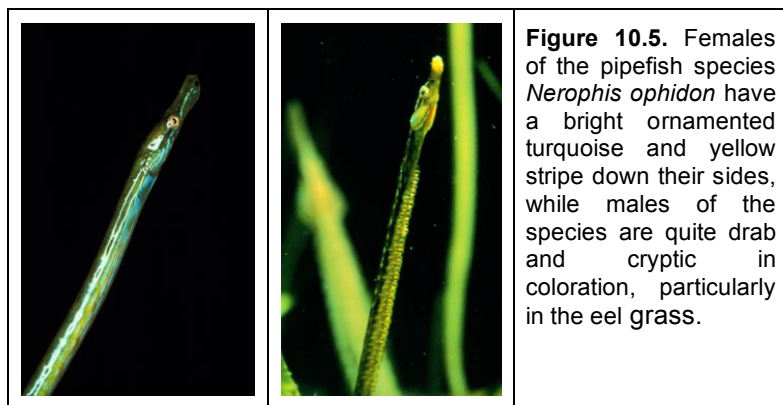
Figure 10.5. Females of the pipefish species *Nerophis ophidon* have a bright ornamented turquoise and yellow stripe down their sides, while males of the species are quite drab and cryptic in coloration, particularly in the eel grass.

Elaborate ornaments in female versus male pipefish are more exaggerated in the species *Nerophis ophidon*. (Fig. 10.5). or *Syngnathus nigra* (Fig. 10.6). *Nerophis ophiodon* females possess a bright blue lateral ornament as well as a skin fold that is used in displays. Rosenqvist and her colleagues tested the role of the female's ornaments and found that male pipefish prefer large females with large ornaments, providing further evidence that females are sexually selected. In *Nerophis ophidon*, the males do not have an elaborate brood pouch and they do not transport nutrients to the embryos. The eggs from the female are carried externally on a brood patch by the male. A **sex-role reversal** in which males provide care, and females possess ornaments suggests that associated reversals of sexual dimorphism in pipefish are related to male choosiness and the intense female-female mate competition. The pattern of sex-role reversal is quite common among species of pipefish leading to even more elaborate female ornaments in the form of skin folds (Fig. 10.6).

Figure 10.6. Female *Sygnathus nigra* with a large skin fold ornament displays to the male (photo courtesy of A. Berglund).

Anders Berglund (1994) tested the idea that a bias in operational sex ratio with many reproductive females and few males leads to male preference for large females. The field data shows a clear decline in the availability of male pipefish from the first to the second reproductive episode in Gullmar Fjord, Sweden (Vincent et al. 1994). Berglund (1993) created male-biased and female-biased tanks of pipefish in the laboratory (Fig 10.8). In female-biased tanks he predicted that males should choose females of large size. In contrast, in a male-biased tank, the preference for large females was expected to be weak. As expected, operational sex-ratio had a striking effect on choosiness of males, causing it to disappear under conditions of a male-biased sex ratio.

Figure 10.7. Sex ratio of *Syngnathus typhle* pipefish in the wild declines from a 50:50 ratio of males to females early in the season to a bias in fewer males available late in the season (from Vincent et al 1994).

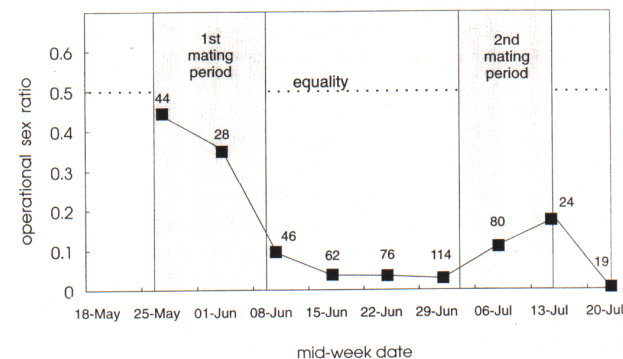**Figure 10.8** Male choice expressed as number of copulations he receives from large or small females. Manipulations of sex ratio in the laboratory indicate that under female-biased sex ratios typical in the wild, males prefer large females. However, when the sex ratio is biased in favor of males, which is quite atypically in the wild, the males do not exercise strong mate choice for large females (from Berglund, 1994).
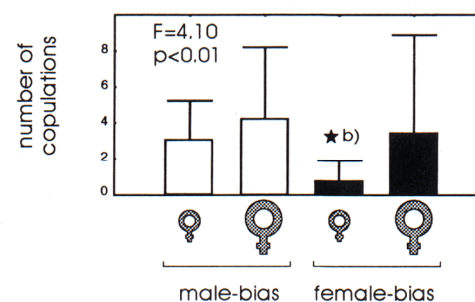
Mate Choice and Material Benefits from Nuptial Gifts

The case of sex-role reversal in pipefish represents an extreme departure from the typical system where females are more often than not the limiting sex. Even though males of most species do not participate in care or the acquisition of energy for young, in some species they have evolved to provide nutrients to the female in the form of **nuptial gifts**. The nuptial gift provided by the male can be a prey item that is offered to the female in the case of hanging flies, or even the male himself in the case of a species of Australian red-back spider, *Latrodectus hasselti*. Male spiders approach the female, attach their sperm transfer organ to the female's genitalia, and then do a back flip into the female's fangs (Forster 1992). While she is eating the male, sperm transfer is completed. Presumably, the body of the male could be used to enhance the fecundity of the female, but confounding this interpretation is the fact that the male's body mass is 1-2% of the females, a trivial snack.

The ultimate gift of life is uncommon in the animal kingdom but its occurrence in insects is common enough to raise eyebrows. Sexual cannibalism is found in spiders, scorpions, the preying mantis, and flies (Polis 1981). Why should males be so self sacrificing? He who retreats after copulation and lives to copulate again, might be more successful in the long run. In nearly all species, the male is rarely a willing participant in suicidal cannibalism, rather many males approach the female with care and caution. An alternative hypothesis is that sexual cannibalism is a result of mistakes made by some males during a clearly dangerous liaison. The female takes advantage of an ardorous male and eats him. No definitive evidence is available to discriminate between these competing hypotheses.

Many insects participate in a less extreme form of gift giving. The gifts range from a captured prey item, to nutrient rich secretions produced by the male. In the case of hanging flies, males offer females a prey item as a gift. The female benefits from a larger prey item as it will provide her with food that she can convert into eggs. The male benefits from giving a large prey item because while she holds onto it and feeds, he transfers sperm into her. The larger the prey item, the longer she feeds, and the longer he has to transfer sperm (Fig. 10.9).

Figure 10.9. a) Larger nuptial gifts in the form of a prey item increase the duration of copulation in hanging flies, *Hylobittacus apicalis*. b) Longer copulation is directly related to number of sperm transferred up to the 20 minute point after which the male should fly off because no further increase to his investment yields any further sperm transfer. This process reflects the action of the MVT (after (Thornhill 1980).
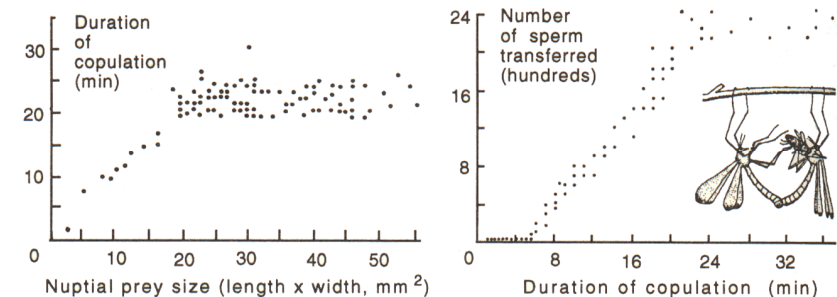

Some of the most elaborate packaging in nuptial gifts is found in male Mormon crickets, *Requena verticalis,* which make a special spermatophore packet that contains the normal sperm packet along with a nutritious protein rich spermatophore (Gwynne 1981). The male offers the female the gift, and places it on her genitalia. The nutritious part of the spermatophore is called a spermatophylax which the female consumes. The business end of the spermatophore contains sperm. The male positions the spermatophore with the sperm side on the female's genitalia. While she feasts on the spermatophylax treat, the sperm is transferred into her reproductive system. The larger the spermatophore packet, the longer the sperm transfer, and the more eggs the male will fertilize in her brood. If a male transfers too small a packet, the female might finish off the protein packet and munch away on the sperm before it is transferred. In such cases the sperm transfer is abruptly terminated.

The female also clearly benefits from the nuptial gift, because she produces additional eggs with the energy that she received in the gift. The more nuptial gifts that she receives, the more eggs she produces (Figure 10.9). She will not receive every gift from the same male, so it behooves a male to present as large a gift as possible as he can then transfer more sperm. Presumably, greater quantities of sperm transferred

translate into an edge against other males during sperm competition which occurs when the female stores different male's sperm prior to laying her clutch of eggs (Figure 10.9).

Figure 10.10. The nuptial gifts of male bush crickets, *Requena verticalis* have a positive effect on the number of eggs laid by females. The spermatophylax is shown on a female bush cricket. The spermatophylax is eaten while sperm is transferred from the sperm ampulla. (data from (Gwynne 1984), figure from Andersson, 1994).
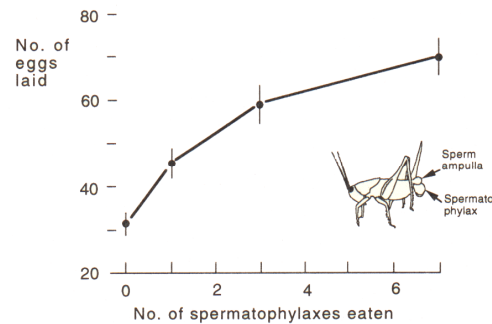
As was the case for pipefish, it is possible to alter the operational sex ratio and male versus female choosiness in Mormon crickets by manipulating food availability, which has a cascading effect on scarcity of the spermatophore resource. When males are fed with high-quality food, males can produce spermatophores quite rapidly. Any male can produce several spermatophores in quick succession. However, when low-quality food is provided to Mormon crickets, it takes much longer for males to produce a spermatophore packet. Moreover, feeding on low-quality food limits female egg production, so a juicy spermatophore is even more of a commodity to females. Under conditions of low food, females might be expected to compete quite intensely for males with a spermatophore, and thus, males should be choosier about the female as function of her size. A male that mates with a large female would be more valuable because she has lots of eggs compared to a small female.

As expected, limiting the availability of food caused a reduction in the number of mates that males obtained and increased the number of mates that females sought (Figure 10.11). When food is limiting males also show a strong preference for the largest females.

Gwynne and Simmons (1990) also tested the effects of food limitation in field experiments. Four cages of 24 males and 24 females received extra food in the form of bee-pollen coating honey-covered stalks of straw.

Four control cages of 24 males and 24 females received dry stalks of straw. Individual Mormon crickets in both treatments also had access to their natural food source. However, clumps of flowering kangaroo paws, *Anigoszanthos manglesii*, are a poor food resource and spermatophylax production by males is limited. In control cages without extra pollen, few males called to attract females (0.4 males on average), male choice of mates was frequent (40% of all interactions), females fought more intensively over the males (20% of all interactions), and few females got more than one mating (0.7 males/female on average). In food-supplemented cages, many males called to attract females (0.4 males on average), male choice of mates was rare (<10% of all interactions), females did not fight over the males (0% of all interactions), and each female mated with many males (1.7 males on average).

Figure 10.11 Number of mates for female and male Mormon crickets, *Requena verticalis*, when fed a high-quality (shaded bars) and low quality food (open bars) in the laboratory. Females seek out more males for copulations when females are subjected to food limitation compared to food abundance. Females seek additional energy for eggs from many male nuptial gifts. However, under food abundance males seek out more females for copulation than food limited males largely because the males can produce many nuptial gifts (Gwynne 1990).
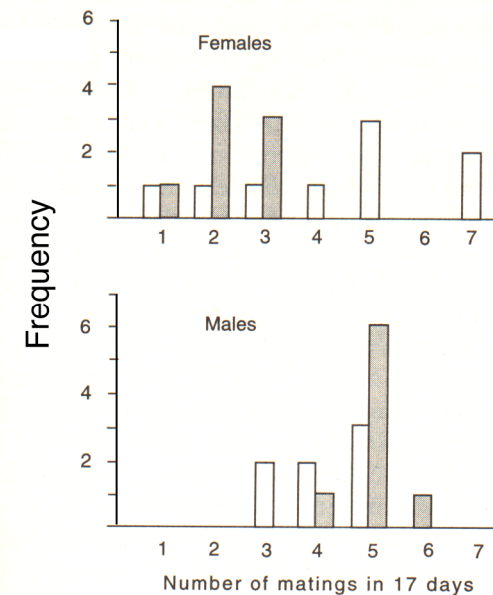
Thus, experiments on operational sex ratio in male and female Mormon crickets, and pipefish (above) indicate that sexual selection is most

intense in the sex, which is in more limited numbers in the population. Furthermore, Gwynne and Simmon's experiments indicate that operational sex ratio is largely driven by the relative amount of energy each sex invests in young (Williams 1966; Trivers 1972). Making Mormon crickets food limited causes males to invest more heavily in the production of young through nuptial gifts offered to the male. Under these conditions, the male can be much more choosy about mates and prefers to mate with large female crickets. However, when food is plentiful, males can easily produce many gifts, and females become choosier over the quality of the male and his gift.

Territory Quality and the Extended Phenotype

Females might choose males on the basis of the quality of the male or the quality of the territory that the male secures. Let's return to the example of bull frogs used Chapter 2. Male bull frogs defend a territory onto which females deposit their eggs. The adult male bull frog then cares for the eggs until they hatch. Howard (1979) demonstrated that female bull frogs tend to mate with the largest male bull frogs and there is a positive relationship between male bull frog size and the number of females that a male secures as mates.

Howard assessed the quality of the male and the male's territory, by tracking the survival of the eggs from hatching to a tadpole. Females have a very strong preference for males that are large in bull frogs, as large males get the most mates (Fig. 3.7). In addition, large males are better able to secure a quality territory on which the male can more successfully rear a clutch of eggs (Fig. 3.7). A large male's territory may have superior thermal resources which allow for proper incubation of eggs, or the large males are perhaps better able to defend their own territory against predators that might eat the eggs.

Territory quality can be considered part of the **male's extended phenotype** (Dawkins 1994). The phenotype of the male is not just parts of his body, but phenotype can consist of any extension of space or object that is a direct result of his superior physiology or strength. Males of many species defend a relatively discrete territory and territory results from male competition with the outcome usually determined by the male's RHP (Chapter 8). Likewise, the attractiveness of a stickleback's nest could be considered the extended phenotype of the male.

Is the female choosing the male for his body size or is she choosing a quality territory? Clouding the issue even further is the idea that the genetic quality of the male may directly influence the survival of his progeny. The male may be large because he has good genes and he passes these genes on to his progeny who likewise enjoy high survival. We could expand the number of factors even further, but three options are entirely enough to illustrate how female choice is a slippery slope of **cause and effect**. Experiments are necessary to determine which of these factors is causally related to a female's choice. Howard addressed the issue of male genetic quality by breeding females to males that varied in size. Howard reared the progeny himself, rather than let the male care for the young. This experiment removes the effect of the male's territory on hatchling survival, but maintains any potential genetic contribution, or 'good genes', that large males might provide to young. Howard found that larger males were no more likely to produce high surviving or fast-growing tadpoles than small males. Thus, the advantages afforded to a female that chooses a large male lies in the advantages of his extended phenotype, the quality of his territory for hatchling survival. However, experimental manipulations of the quality of the male's territory remain to be carried out in bull frogs.

Choosing males based on their territory is common. Dragonfly males that defend the best egg-laying sites get the most mates (Campanella and Wolf 1974). Female wrasses prefer to mate with males that hold deep-water territories. Territories located in deeper water are thought to have lower rates of egg depredation (Jones 1981). Male red-winged blackbirds, *Agelaius phoeniceus*, which defend quality territories with suitable vegetation, attract more females (Searcy 1979). The issue of territory quality is so essential for females that use the territory to feed their nestlings that we will take up the topic again in the Chapter 11 on Conflict, where a test of the **direct benefits** of a territory versus the **indirect genetic benefits** of mate choice for good genes is described for the side-blotched lizard. We will first have to work out paradigms for testing for the indirect benefits of good genes, which is described below.

Why Female Choice Experiments are Necessary: Cause and Effect

Female choice experiments seem pretty obvious. Put two males that vary in quality in front of a female and let the female choose between the

two. However, the controversy between alternative theories of mate choice makes manipulative experiments critical for determining cause and effect. A female can choose a male on the basis of a number of potential traits, and male traits might be correlated with one another or with the female preference *per se* (Andersson 1994; Sinervo and Basolo 1996). It is essential to perform manipulative experiments of the male trait to isolate the effects of a specific trait on preferences expressed by females.

Figure 10.12 Andersson's (1982) classic manipulation of tail length in widowbird, *Euplectes progne*. The average number of females on the territory of males in each treatment groups is shown prior to manipulation of tail length. After manipulation, males with elongated tails enjoyed enhanced reproductive success: the number of females on their territories is higher than the other groups. (from Andersson, 1996)
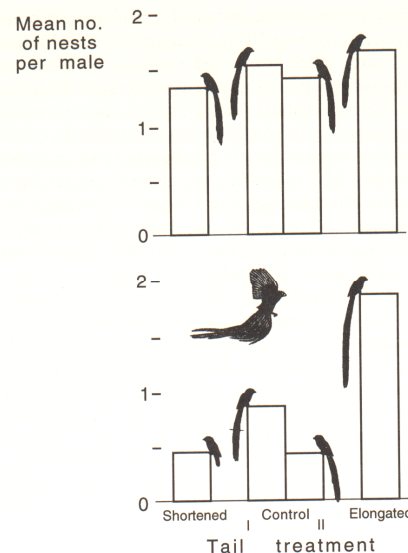
Time and again researchers have demonstrated female choice in experiments. Cutting and pasting a larger ornament on some males and reducing ornament size in other males is a simple, but effective way to uncouple male quality from the effect of the ornament. Often females show a preference for **supernormal stimuli**, or ornaments that are so large they would not normally encounter males with such ornaments in nature. Malte Andersson (1982) carried out such an experiment in the widowbird, *Euplectes progne*. Before the experiment, females chose the groups of experimental males with nearly equal frequency. Andersson then gave female widowbirds the choice of staying with "cut-and-paste" males that now varied dramatically in tail length: some males got smaller tails (short-treatment), some were cut and re-glued (control) some remained unaltered, and others received elongated tails (long-treatment) (Fig. 10.12). After the manipulation, males with the elongated ornament were chosen by females at a much higher frequency than the

males with the cropped ornaments. Unmanipulated control males, sham-manipulated controls, and males with shortened tails had similar numbers of females on their territory. In addition, Andersson's experiment also showed that males with shortened tails did not lose their territories, just the mates on their territories. This observation confirms that female choice is the selective force driving long tails in widowbirds, not male-male competition.

Many organisms choose mates based on the sound of the opposite sex's call, instead of using the visual system. In such organisms, the ability to use recorded male songs in a "playback" style experiments is ideal because one can remove all aspects of the male phenotype except for the salient aspects of the song itself (Charalambous et al. 1994). You can even engineer the song quality and manipulate the same male's song and see that female choice is affected by such digitally engineered songs (see Chapter 5, studies by Gerhard 2005 on acoustic preference of hylid frogs). This controls for quality effects within a single male. For example, female crickets prefer a long song type over a short song. Male crickets produce a trill-like song by rubbing their legs against their dome-shaped wings. The dome-shaped wing resonates a song for a female's acoustic senses. A female tends to walk towards a speaker that is playing a long song compared to an adjacent speaker that is playing a short song. Presumably, a male producing a longer song provides the female an indication of the male's quality.

Cut-and-Paste Experiments on the "Extended Male Phenotype"

Females also choose males on the basis of his extended phenotype. Shrikes are a carnivorous bird of the desert with a penchant for skewering lizards onto thorns or barbed wire. For years, naturalists used to think that shrikes store these lizards as a food stash. It was thought that the shrike was storing the lizard carcass for food during lean times when lizards, one of their chief food sources, were scarce. The problem was that shrikes left lizards on thorns until they had dried into tough, shriveled-up strips of scales and bones surrounding a chunk of dry meat. Unless shrikes like lizard jerky, dried lizard-ka-bobs, or lizards-on-a-stick, something was amiss with the "food larder" hypothesis.

The answer was solved when Yosef and Pinshow (1989) manipulated the number of skewered lizards on a male's territory. The males with

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lizard carcasses added to the thorny bushes on their territory had females arrive on their breeding territory earlier and significantly more females nesting on their territories than the males that had their lizard ornaments removed by Yosef. Presumably, females gauge a male or the quality of his territory by the number of lizards that he has skewered. This punk lizard jewelry decorates the male's territory and tends to drive a female shrike's mate choice.

<< Fig. 10.13 to get picture from Yosef >>

Paying the price for ornaments and advertisements

Charles Darwin was the first to realize that either form of sexual selection, female choice or male-male competition, was likely to lead to the evolution of elaborate structures which reduce survival. As we have seen in the chapter 8, male-male competition results in direct survival costs from the possession of a weapon *per se*, and its use in contests. While lethal fighting is rare in the animal kingdom, it still occurs in many species. It is not uncommon to come across the skeletons of two deer that are locked in the death grip by their entangled antlers.

Even if battle is not lethal, the 'war of attrition' can leave both combatants that are fighting over mates in a weakened physiological state. Their immune systems become suppressed (Folstad and Karter 1992), and their health declines to the degree that death may be just around the corner. In addition, the physiological mechanisms that produce elaborate ornaments can have indirect costs which reduce survival. Antlers in deer and moose require growth each season because they are shed every fall in preparation for the long and lean winter. The development of many secondary sexual traits in vertebrates requires testosterone. Because production or development of a larger structure or capacity to sing a long song often requires higher levels of testosterone, then elevated levels of such hormones might lead to survival costs because of a pleiotropic relationship (see Chapter 2) between survival and the sexually selected traits governed by testosterone production (see Chapter 8). The reduction in survival arising from male-male competition is not all that enigmatic given that eliminating your rivals is one of the primary goals of male-male competition.

Why should female choice *per se* promote the evolution of ornaments in males that carry heavy survival costs? Are doe choosing male stags based on the size of their antlers, in addition to the clear role antler size plays in male-male contests? The simplest answer is that male ornaments are used to attract females and in male competition. A female watching a male contest is likely to choose the victor, and her choice may be directly tied to the outcome of male-male competition. In some animals, structures may be used as an ornament to attract females and an armament in male-male competition. Many researchers assume that because a structure is not used directly in battle, that structure is used primarily by females to choose a mate. In chapter 8, I discussed how badges of status might evolve as an information signal which announces the male's physiological vigor to rivals. The male does not use his throat color or bright plumage in battle, but the male might use such badges to intimidate rivals and avoid costly battle. The badge evolves as a relatively **honest indicator** of the male's physiological vigor. Keep in mind that it is very difficult to disentangle issues of female choice from issues regarding male-male competition.

Many studies of male ornaments have often focused on structures that appear to have a purely "attractive" role, because these experiments are easy to conduct in laboratory choice trials. In contrast, experiments on male-male competition often require an experiment in the wild because the male's territory may be essential to motivate the male to perform (see Chapter 11). In addition, ethical concerns (Huntingford 1984) for a scientist that instigates a "cock fight" in which one combatant may be injured, have limited the number of experiments where male-male competition has been directly linked to male fitness.

Some ornaments are clearly used in only male-male competition as badges of status, while other ornaments appear to be only used during female choice. The only way to make such distinctions is to perform experiments that test the role of the ornament as a badge of status used in male-male competition (e.g., see throat-color experiments on lizards, Chapter 8) or an ornament used in female choice (e.g., widowbirds, above). For example, experiments on the bright red shoulder patch of red-wing blackbirds, *Agelais phoeniceus*, indicate a very clear role of the ornament in male-male competition, but no apparent role in female choice. Male red-wing blackbirds with the red patch painted over with black would more often loose their territory to a floater male, than

control males in which the patch was left intact (Peek 1972; Smith 1972). However, females do not appear to exercise choice regarding the ornament. Similar badges in other species of blackbirds apparently have little effect on male-male competition. For example dying a male yellow-headed blackbird's, *Geothlypis trichas*, head entirely black has no effect on his ability to hold a territory. Nor does the presence or absence of the 'yellow-head' badge appear to affect the harem size of a male yellow-headed blackbird compared to the harem size found on the territory in previous seasons field work (Rohwer and Røskaft 1989).

Ornaments may also have a cost because they attract predators. The ornaments found on the birds of paradise are largely used in displays to females when the males are on leks. Such elaborate and colorful male ornaments undoubtedly attract predators as much as they attract the females (see Chapter 14). Some of the best evidence of the cost of male ornaments comes from work on the guppy, *Poecilia reticulata*, which inhabits the wild streams of Trinidad.

Male guppies possess spots of varied color that have been clearly implicated in female choice. Males with more spots and longer tails attract more females and higher copulatory success (Bischoff et al. 1985). The spots can be **structural colors** such as blue, iridescent, or bronze. Pigments created by structures in the fish reflect and refract light much like mirrors and prisms alter the wavelengths of light. The spots might also be orange, red, or black, which are created by **pigment granules**. Some of the colors used to attract females, such as orange, are derived from carotenoid pigments that are found in the food eaten by the guppies. The presence of spots and the colors of spots are governed by a large number of X- and Y-linked genes that are only expressed in adult males (Houde 1994). The structure of signals is discussed in Chapter 13.

→ **Figure 10.14.** An artificial selection experiment in which tanks of guppies, *Poecilia reticulata*, were exposed to a very dangerous predator, *Crenicichla alta*, a fish that can eat the adult guppies, or a less dangerous predator, *Rivulus hartii*, a fish that only eats juvenile guppies. A control line of fish was maintained in population tanks without the predator. The action of dangerous predator in the breeding tanks of guppies selects for males with fewer ornamental spots. Sexual selection appears to favor highly spotted males in control tanks and in the tanks with the less dangerous predator (from (Endler 1980). The fish along the side illustrate the variation in spot number (from Andersson 1994).

In populations that are relatively free of predators, males are much flashier in color compared to males in guppy populations with a high risk of predation. The level of predation among guppy populations is dictated by how far the populations are found upstream. In the upstream pools, a small ineffective predator called *Rivulus hartii* can eat the offspring of guppies, but has trouble taking down an adult. In the lower reaches of the stream, a large and fast predator called *Crenicichla alta* can easily gulp down guppies like fraternity members choking down goldfish at an initiation ritual. As you travel upstream, you will be less likely to encounter the dangerous predator because the waterfalls gradually filter out the large-bodied *C. alta*. At some point upstream, *C. alta* disappears entirely.

In the areas upstream, male guppies develop quite gaudy ornaments because they are relatively immune to the effects of predation. In what has become a classic field test of theories of natural and sexual selection, John Endler (1980) introduced predators to upstream pools where predation pressure was naturally low. Endler (1980) transplanted the dangerous *Crenicichla alta* to the upstream pools and within a few generations, the male guppies became much drabber. Natural selection caused by predation works against the force of sexual selection that favors sexy coloration in males. Endler then followed up these field transplant experiments with carefully designed laboratory experiments
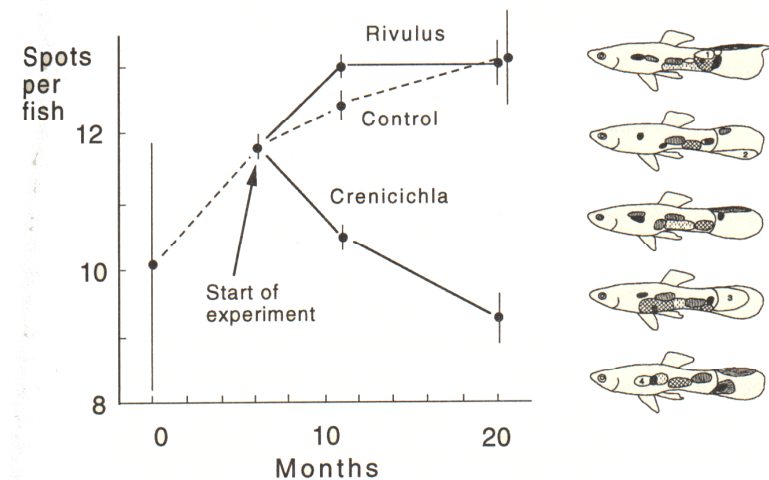
in artificial ponds. Within a few generations after the introduction of the two kinds of predators, the coloration of males was reduced in the presence of the dangerous predator, but not in the presence of the less dangerous predator.

In a series of comparisons among populations that vary in the intensity of predation, Houde and Endler (1990) found that the selection against bright orange male coloration may also affect the degree of choosiness that females express for orange. In areas where the predation regime is higher, males have much less orange, and females appear to have evolved to prefer males with less orange. In contrast, when predators are rare the females evolve to prefer males with a great deal of coloration. Houde and Endler (1990) go on to state that the differences among populations are not strictly due to only the presence or absence of predators.

The streams also vary in the amount of turbidity, and thus environmental factors such as the amount of light of varying wavelengths that penetrates into the stream may also limit the ability of males to use bright orange as a color to attract females. Orange and red wavelengths of light only penetrate into relatively shallow and clear water. Under murkier conditions other pigments might be used to attract females. We will take up the design of male ornaments in Chapter 13 when we consider the physics of signal propagation, and neural and sensory constraints on signal reception.

Figure 10.15. Strength of guppy female preference as a function of the amount of orange color in several streams (different symbols). The strength of female preference for orange is positively correlated with relative amount of orange in males (from Houde and Endler, 1990).
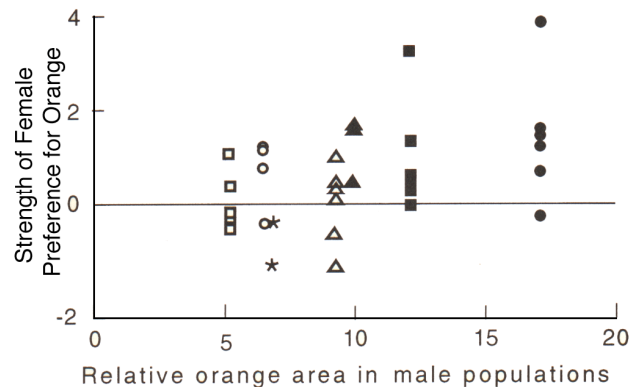
Models of Mate Choice and Sexual Selection

The examples of male nuptial gifts to females are a case of **direct selection** on female choice. A female that chooses a male with a large gift receives a direct benefit that might enhance her fecundity. There is no controversy regarding selection that causes a female to choose males on the basis of such direct benefit. A female that is choosier will produce a larger clutch or better quality offspring and thus leave more descendants with choosy genes in the population.

Darwin was the first to point out that female choice can lead to sexual selection for elaborate male ornaments for reasons other than a direct benefit. A female that chooses a male with a large ornament is not necessarily receiving a direct benefit from the ornament. Yet how do such choices become so prevalent in a species such as the gaudy peacocks that evolved from a drabber ancestor? Male ornaments evolve to such a large size that there must be a large survival cost for the male.

A variety of models have been developed to explain how **indirect selection** on female choice can lead to ornaments in males, that have no direct adaptive function for the female. Ronald Fisher is credited with his succinct description of how mate choice by females can lead to a selective runaway that favors ever more elaborate male traits despite their debilitating effects on male survival. The indirect selection on female choice arises from a powerful genetic correlation being formed between female choice and male ornaments by the process of assortative mating. Fisher was a brilliant mathematician who added a great deal to the understanding of evolution (Chapter 1). His capacity for intuitive arguments was unparalleled in evolutionary biology and his writings are a challenge to read. Such was the case with Fisher's (1930) intuitive argument of **runaway process** that I describe below. A formal proof of runaway sexual selection has only recently been constructed by two theoreticians, Russell Lande (1981) and Mark Kirkpatrick (1982), who derived on similar arguments, quite independently, at virtually the same time, and fifty years after Fisher's original writings.

In 1975, Zahavi came up with an alternative theory for the evolution of male ornaments and female choice in which the ornaments are a form of 'handicap'. Zahavi's (1975) ideas have been reformulated by many other researchers into a more general **"good genes"** theory for the

evolution of female choice. A male that develops and carries an ornament into adulthood must also carry a large number of good genes, not just those genes that control the ornament size. Such males would be good mates for a female because the size of the ornament is an honest indicator of the male's quality. Because the female choice for a male's more elaborate ornament has an indirect benefit for her offspring, the good genes models are another form of **indirect selection** on female choice similar to Fisherian runaway. Zahavi's (1975) ideas precipitated a heated controversy in behavioral ecology and evolutionary biology that has not abated. Numerous models were developed during the ensuing decade of the 1980's to try to either refute good genes models or prove the alternative models such as Fisherian runaway (Kokko 2006).

We can distinguish these two classes of models by the relative utility of ornaments from the perspective of the female. In runaway models females just get a sexy mate, which produce choosy daughters and sexy sons in the next generation. In good genes models she gets a sexy mate, and she gets good genes from the male to pass down to her offspring. Which model is correct? Only empirical data can resolve the debate as a variety of plausible models can be found that support both views for the evolution of female choice under sexual selection. The dynamics of sexual selection in either good genes models or runaway are complicated (derivation of runaway given in Chapter 3).

If the genes that code for female preference and the genes that code for the male trait become **genetically correlated** by sexual selection. A son with a large ornament, will also get alleles for female preference because their own mothers had a preference for ornamented males. The converse is true for a son with a small ornament -- he was born from a male with a small ornament and from a female with no preference for ornaments (the only females a small ornamented male mates with are non-choosy females). Thus, fathers (and mothers) will likewise pass on both sets of genes to male and female progeny. Evidence of runaway manifests as a positive correlation for the preference that daughter's express, and the ornament size expressed by the sons (Fig. 17). The reason we must measure the traits in the two sexes of progeny is because daughters do not express the ornament, but son's do. Conversely, daughters express mate choice while son's do not. Many behavioral traits have this kind of **sex-limited expression**.

A key aspect of sexual selection that I have ignored so far, are the survival costs of male ornaments. As seen above, the impact on survival due to male ornamentation can be substantial. The additional survival costs of ornamentation only have a modest effect on the dynamics of sexual selection, Fisherian runaway sexual selection is still possible.

Figure 10.16. The strength of a genetic correlation set up by assortative mating (panel **A**) is a key factor that determines if a stable equilibrium between female preference and the male ornament is achieved (as in panel **B**), or whether the Fisherian runaway process leads to trait exaggeration (panel **C**). A) Assortative mating between female choice and the male trait will set up a genetic correlation (see Side Box 10.1). **A)** A genetic correlation is revealed by a breeding experiment in which we rear progeny from one sire (or dam) and compare the correlation between a brother's trait and sister's preference. Daughters from some sires have a preference and their brothers have large male ornaments (points in upper right corner). Daughters from other sires have a weak preference and their brothers have small ornaments (points in lower left corner). The strength of this genetic correlation (slope=B/G) will determine whether or not runaway sexual selection takes place (panel B or C). However, the evolutionary outcome also depends on the balance between two factors: the strength of female preference for large ornaments and the strength of natural selection that favors survival of male with small ornaments. B) If sexual selection and preference is weak, and natural selection is strong then evolution results in a stable equilibrium (see text). If populations begin at some point above the line, the population will rapidly evolve towards the equilibrium, while those below the line will rapidly evolve towards the line. The approach to the line of equilibrium (lines with arrows) follows the slope dictated by the genetic correlation (Slope=B/G), which is set up by the process of mating. C) However, if the preference is strong relative to the force of selection, the population can evolve rapidly away from the equilibrium in a runaway process that leads to either trait exaggeration (above the equilibrium lines), or to elimination of female preference and male ornaments (e.g., below the equilibrium lines) (from (Arnold 1983).
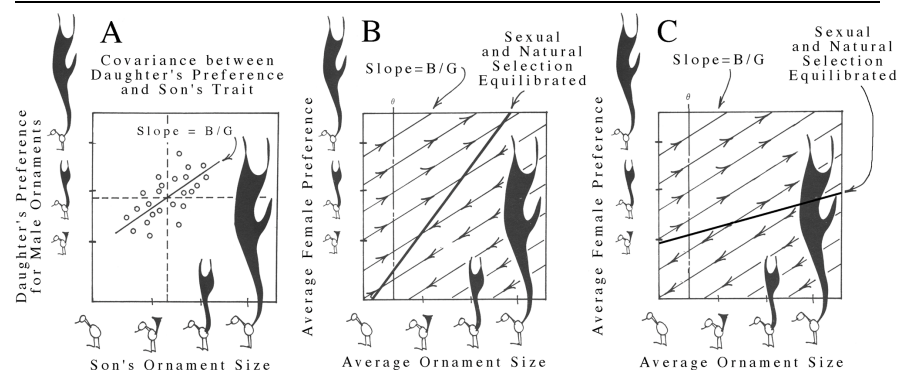
Even with a survival cost, Fisherian runaway process can carry the male ornaments and female choices to absurd levels that are epitomized by the bizarrely 'dressed' male birds of Paradise (Figure 10.1). Whether or not a runaway process takes hold of a population depends on the strength of female mating preferences relative to the strength of survival costs of the ornament. Thus, the survival costs are important to the outcome.

If female preference for large male ornaments is relatively weak (any male will suffice regardless of ornament size), and survival costs of a large ornaments is strong, then a stable equilibrium between sexual and natural selection is achieved (Figure 10.17.B, 10.18). However, evolution does not carry the population to a unique stable equilibrium, rather female choice and male preference come to rest on a 'line of equilibria. Movement towards the line of equilibria depends on the placement of the population relative to this line before the process of sexual and natural selection began. The approach to the line of equilibria follows along a pathway that is dictated by the strength of genetic correlation formed by assortative mating. Anywhere along the line of equilibria, the force of sexual selection exerted by female preference balances exactly the force of natural selection (see Figure 10.18). In some populations, strong female preference balances the strong survival costs in males with large ornaments. In other populations weak female preference supports only a modest survival cost in males, and correspondingly small ornaments.
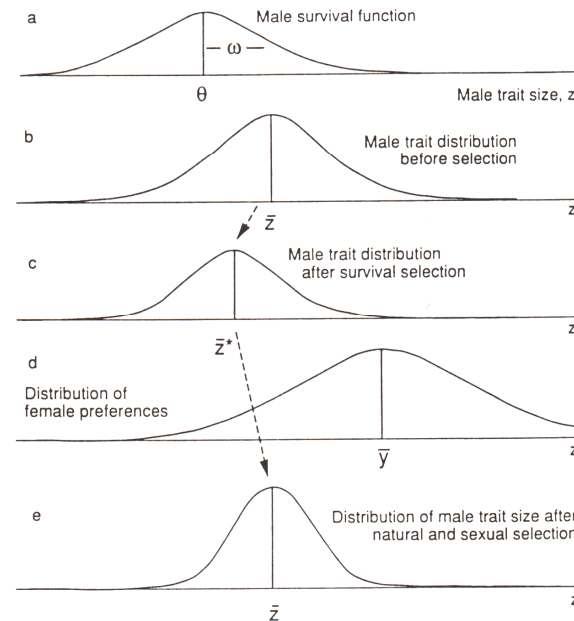

Figure 10.17. What happens at the equilibrium between sexual and natural selection? a) The function describing male survival has an optimal value for the ornament, Θ, which favors males with small ornaments relative to b) which depicts the population distribution with mean, $\bar{z}$, before survival selection takes place. c) Selection reduces the mean size of the male ornament to $\bar{z}^*$. Males with too large an ornament are winnowed out of the population. d) However, males that manage to survive to maturity with a large ornament have an advantage arising from female preference. The distribution of female preferences in the population is such that females prefer males with large ornaments ($\bar{y}$). e) Sexual selection carries the male trait back to $\bar{z}$, where it was before an entire generation of selection took place (Andersson, 1994).

ludicrously exaggerated male traits and very strong female preferences for these traits. As the ornament becomes exaggerated to enormous size, males suffer a larger survivorship cost to the ornament. However, female preference can also take the population to another extreme; a reduction in ornament size, which depends on whether the mean value of the trait in the population is above or below the line of equilibria between sexual and natural selection. The mean values of male ornaments in the population will 'runaway' to enormous size if the mean value for both female preference and the male trait falls above the line. If the mean value for both traits is small the runaway will carry the population in the other direction and eliminate female preference for ornaments as well as the male ornament.

Conditions for dramatic runaway sexual selection are possible when female preference for exaggerated ornaments is strong, and the opposing force of selection against large ornaments is weak. Intuitively, we can think of females having such a strong preference that they only mate with males that match this preference. This choice can overwhelm the stabilizing force of natural selection. The population rapidly evolves to

Thus, a number of interesting evolutionary outcomes are possible under the Fisherian model of sexual selection: 1) the population can become sexually dimorphic with greatly exaggerated males, 2) the population can achieve a middle ground of dimorphism with modestly exaggerated males, or 3) the male ornaments can become eliminated entirely. All of this happens rapidly in the span of hundreds of generations. It is unlikely that we will see such fleeting change in nature, unless we create it

ourselves in the confines of a laboratory experiment. In light of the speed of the runaway, it is not surprising that little direct support has been found for the process of runaway in nature. Most populations in nature are expected to be at the equilibrium where balance is struck between sexual and natural selection (Figure 10.15). While number of spots on a male guppy may vary among populations, each population is expected to be in equilibrium. Endler's manipulation of the predation environment alters the equilibrium (e.g., males with lots of spots face a dangerous predator), however the system rapidly returns to the new equilibrium (see Figure 10.14).

Pattern and Process: Evidence for Runaway Sexual Selection

One of the key predictions regarding the action of Fisherian runaway sexual selection is that genes for male coloration should become genetically correlated or linked to genes for female preference (Figure 10.16). Tests of this first simple prediction have taken two approaches. First, researchers have searched for a positive correlation between the preference expressed by daughters and the degree of male ornament expression in sons. Second, researchers have selected on the male trait, and if female preference is genetically correlated, the female preference should indirectly respond to selection on male ornaments. The first approach tests for *pattern* in a genetic correlation. In contrast, the second approach tests for the *process* by which male trait and female preference change in unison (Chapter 3, artificial selection by Houde).

Bakker (1993) measured the genetic correlation between red coloration in stickleback males, and female preference for red coloration. When he reared the progeny of males that varied in the degree of red coloration, he found that males with more red produced red sons, and they also produced daughters that had a strong preference for red. Males with very dull coloration tended to produce dull sons, and daughters likewise tended to prefer dull-colored males. Daughters and sons receive genes for female preference and degree of male ornamentation as a genetically coupled set of traits from their parents.

The linked genes that progeny receive are correlated from previous generations of selection. The **pattern** of a positive genetic correlation is very strong **comparative evidence** that traits under sexual selection are genetically correlated in stickleback fish. This pattern is consistent with

the hypothesis of runaway sexual selection. However, as we will see below the pattern is far from conclusive as a genetic correlation could also be produced by alternative mechanisms of good genes models.
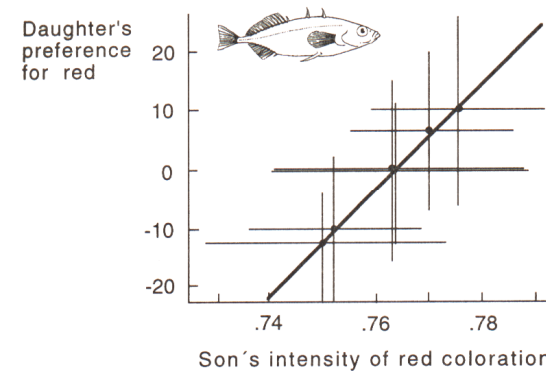

Figure 10.18. A genetic correlation between the son's intensity of red coloration and the daughter's preference for red color provides evidence for assortative mating leading to a genetic correlation between female choice and male traits. (from Bakker 1993).

Good Genes Models

There are now a vast number of different **good genes models** on the market, but all models share a common feature (Pomiankowski 1988; Andersson 1994); females choose males with elaborate ornaments because the ornaments *indicate* superiority of the male's genotype which can indirectly benefit her offspring. For example, the female might use ornaments to determine whether or not the male possesses parasite resistance that might be passed on to her progeny. Only males that remain parasite free are healthy enough to produce large ornaments. The models are thus, also referred to as **indicator models**. The female receives no direct benefit such as enhanced fecundity from choosing these ornamented males, but rather she receives an *indirect benefit* in the form of genes that she can pass on to her offspring. Good genes models and runaway process models will lead to a genetic correlation being formed between the genes for the male trait and the female choice (see Side Box 10.2). Both models have non-random mating occurring between the sexes as a function of their mutually complementary ornaments and preference. In good genes models, a third class of loci become correlated with the male traits and female choice and these are what we refer to as good genes.

Side Box 10.2 - How Do Good Genes Differ From Runaway?

The key feature of runaway models of sexual selection is that two loci evolve in tandem. A locus for the male trait codes for a large ornament (*A*) compared to the normal-sized ornament (*a*). A second locus codes for the female preference where an allele for preference, *B*, causes females to choose *A* males, while females with allele *b* mate with *A* and *a* males at random. These same two loci are essential for both good genes models and runaway models. All good genes models lead to a genetic correlation between the male ornament and female choice similar to Fisher's prediction of the correlation by runaway sexual selection. Thus, the presence of a genetic correlation between male ornaments and female traits in a population does not provide us with the empirical data necessary to discriminate between runaway versus good genes processes acting on the evolution of female choice. Both of these models also assume that possession of the ornament (e.g., genotype *A*) leads to a survival cost.

Good genes models differ from runaway models in that they also assume the existence of a third class of loci. Males with alleles *C* have higher vigor or viability than males with alleles *c*, which have poor vigor or viability. Genes that code for vigor allow males to develop large ornaments. Alternatively, the same good genes could also enhance viability. A male with a large ornament and good genes have high survival to maturity compared to male with large ornaments, but poor genes. Either of these two physiological mechanisms, vigor or viability, will result in males with large ornaments at maturity being a select group of males. They naturally contain good genes, otherwise they wouldn't survive or be vigorous enough to grow a large ornament.

Let's dissect the process in more detail (Andersson, 1994), but we will only consider viability selection and ignore vigor effects on the ornament. Because ornamented males bear a survival cost to begin with, those ornamented males that also carry allele *C* are more likely to survive to maturity than ornamented males that carry allele *c*. Whereas males with normal-sized ornaments can also possess the good gene, *C*, or the poor gene, *c*, they *do not bear a tremendous survival cost to* maturity. Thus, the survival of normal-sized males is not dependent on the good gene -- all survive to maturity. Females with a preference (*B*)

for the ornament then are likely to mate with males that only carry the *C* allele, and pass this on their offspring. Females with a preference (*b* allele) mate at random and mate with males that can either carry the good allele or not carry the good allele.

In a randomly mating population with no sexual selection we would expect to see lots of combinations of the genes A, B, and C (e.g., *ABC, ABc, AbC, Abc, aBC, aBc, abC, abc*). However, in a population that experiences the force of 'good genes' sexual selection many of these genotypes become over- or under-represented. For example all three alleles, *A*, *B*, and *C*, become greatly over-represented in sons and daughters of ornamented males and choosy females. Females that prefer (*C*) males with large ornaments (*B*), mate with males with good genes (*A*), and pass all three on to their offspring (e.g., ABC). Conversely, females with no preference (e.g., allele *b*) are just as likely to get the dregs (e.g., a male with the small ornaments, *a*, and poor genes, *c*) as they are to get good genes (e.g., a male with small ornaments, *a*, and good genes, *c*). Very few of the non-choosy females get good genes males that have large ornaments, as they are scooped up by the choosy females. Thus, the frequency of combinations *a*, *b*, *c* and *a*, *B*, *c* also become over-represented. Few of the progeny of the next generation carry the combination *aBc* (males with large ornaments, but poor genes do not survive) or the combination *aBC* (choosy females go for males with big ornaments not small ornaments). These combinations get under-represented in subsequent generations. In a fashion reminiscent of runaway sexual selection, the ornamental alleles (*A*) and female choice (*B*) can hitchhike a fitness ride to high frequency through their genetic associations with the viability alleles (*C*). Because the overall dynamics of the process of good genes models is similar to runaway, it is difficult to discriminate between the two models. The only empirical evidence that discriminates between the two is the existence of good genes being linked to the male ornament. Empirical tests of the two models of sexual selection have focused on this key piece of evidence: do ornamented males produce high quality offspring.

Figure showing how combinations (*AbC, Abc, ABc aBC, aBc*) get winnowed out of the population while (*abC, abc*) and (*ABC*) remain. The combination *ABC* increases.

A male must harbor such genes if he is able to survive to adulthood with his energetically expensive ornament that exposes him to predation risk. The ornament becomes a form of 'honesty in advertising.' Presumably, a male with an elaborate male trait would have to be quite superior to be able to survive to reproductive age with the large trait. He should have many genes that are related to his overall vigor, but that are not necessarily related to *genetic control* of ornaments. Rather the *environment* alters ornaments as a function of the quality of the male.

Whereas runaway models and indicator models both lead to the formation of strong genetic correlations by the process of non-random mating, the models differ in the proximate source of variation in male ornament size. In the case of runaway, the male trait is assumed to be genetically transmitted. In the case of good genes, variation in the indicator trait, the ornament, does not arise from variation in the genes controlling ornament size (Pomiankowski 1988; Iwasa et al. 1991). The ornament develops to a large size because the male is physiologically vigorous. Vigor arises from many genes. If indicator models were at work, all males in the population could potentially develop a large ornament because genes that control ornament development are the same among males. However, males that are endowed with advantageous alleles develop a larger ornament than those males with inferior growth alleles. Indicator alleles do not just promote good growth, but they also can promote high survival to maturity (see Side Box 10.2). The interactions between a male's genes controlling general physiological vigor and survival and those that specifically promote ornament development allow females to discriminate against males with small ornaments in favor of males with large ornaments. In the examples described below, I discuss other kinds of indicators besides good genes.

In summary, the runaway model assumes less about the process of sexual selection than the good genes models. It is more similar to a *null model* of sexual selection (Ryan 1997); runaway *will happen if* some females choose males with ornaments and ornaments and female choice are heritable. Good genes are considered a more complex *alternative model* that requires additional empirical support; males with ornaments produce quality offspring. In the absence of evidence in favor of good genes, we reject the more complex model of good genes in favor of the simpler model of Fisherian runaway as being responsible for the

exaggerated male trait, provided other aspects of the sexual selection are consistent with runaway (e.g., presence of a genetic correlation between the male trait and female choice).

Peacock Tails and Peahen Choices

Marion Petrie (Petrie 1994) set out to test the idea that females might choose males on the basis of some sexually-selected trait. Petrie hypothesized that a female's choice of ornament might have indirect genetic benefits for her offspring. Again the problems of correlation versus causation come into play. Might a female who has a tendency to search out the best male (not an easy task), also be a robust specimen in her own right? She might also have above average genes compared to other females. Such a genetic background might allow her to gain access to males of extraordinary ornamentation when other females are less likely to attract his attention. The male with the ornament could also be making choices of a female that are opaque to us.

To remove confounding effects of female quality, Petrie had to control the matings between peahens and peacocks. Rather than carry out these difficult experiments in the jungles of Asia were peacocks and peahens occur naturally, Petrie carried out the experiments in Whipsnade Park, a zoological and botanical garden in London. In Whipsnade Park, Petrie could more carefully control breeding between peahens and peacocks, and closely monitor growth and survival of progeny. Petrie first established the qualities that make males attractive to peahen. Based on such choice experiments, she identified what females preferred in a mate. Females found males with a large average spot size on their tail quite attractive (Petrie et al. 1991; Petrie 1994). Even though she let peahens freely express their choice to identify quality males, she did not let the females copulate with their mates, instead, she arranged the matings randomly. Petrie predicted that offspring from males with large spots would be robust in their growth rate, or perhaps in their survival as chicks.

Random mating between females and males as a function of their ornaments (and choice) allowed Petrie to disentangle the confounding effects of female quality and female choice from the genetic contribution that the male might make toward offspring. Both of Petrie's predictions were borne out (Petrie 1994). When she randomly mated

peahens to the males, the sires with larger spots on their tail ornaments tended to produce chicks that had both high growth rate and high survival, suggesting that males with larger ornaments harbor genes that are good for progeny survival. Fathers with smaller spots on their tails produced poor growing offspring that also had low survival. This example provides clear evidence that the male ornament is correlated with genes that provide an indirect benefit to the growth and survival of the female's progeny. Female peahens should choose males with large spots on their tail, and peahens do indeed favor males with large spots, because of the indirect benefit to progeny growth and survival.

Figure 10.19. Peafowl, *Pavo cristatus*, chicks from fathers with a larger mean spot size on their tails a) survive better and b) grow faster than peacock's chicks from fathers with a small spot area. A representative spot on the tail is shown. The tail of a peacock contains an enormous number of spots forming an elaborate train that males can fan out to attract peahens. (from Petrie 1994).

Parasites, Good Genes and Swallow Tails

Hamilton and Zuk (1982) proposed that species under strong sexual selection should have a higher incidence of parasitism compared to non-showy species. They reasoned that a species undergoing sexual selection would favor male traits to such an extent that the male's physiological state would become debilitated, causing them to be more susceptible to parasites, but not all males in the species would be so affected. Because developing ornaments is so costly, only a male in good health could develop brightly colored ornaments. Those that had the brightest ornaments would presumably be parasite free, with genes that might protect them from parasites. Females that mate with the brightly ornamented males would acquire "parasite resistance genes" for their offspring. The host population and the parasite species are in an
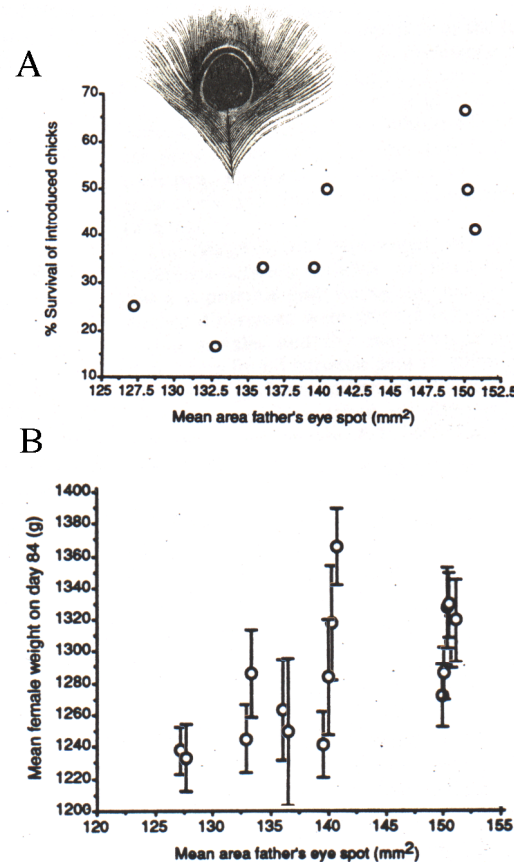
evolutionary struggle of sorts. The parasite is rapidly evolving genes to break down the host's defenses, while the host population is evolving new resistance genes to fight off the parasitic infections. These genes in the host are also linked to male traits by a process very similar to the good genes model outlined in Side Box 10.2.

Hamilton and Zuk made the following predications. Species that were not as showy would not be under such strong sexual selection, and most males would be capable of fighting off infectious agents. They speculated that these species would not be as likely to have a high parasite load. Hamilton and Zuk tested their ideas by performing a comparative experiment in which they ranked a male of each species for showiness from 1-6 (1 being least showy, 6 being the most showy) and correlated "showiness" (e.g., degree of sexual selection) with data on the risk of being parasitized. They found a very strong correlation between parasites and showiness. However, other studies have failed to find a similar correlation.

While Hamilton and Zuk's idea is ingenious, there are alternative explanations of the pattern of high parasitism in sexually selected species. Showy species also tend to be the species in which males are highly polygynous (they have numerous female partners). Non-showy species tend to be monogamous (usually one female partner/male). If the risk of infection by sexually transmitted diseases is a function of the mating system, then one would expect polygynous, showy species to be more likely to have sexually transmitted diseases compared to the more mate-faithful monogamous species. A polygynous male has many partners from which to pickup or transmit the infection. Herein lies the problem with purely correlational studies. There could be many causes for the pattern, not necessarily the "cause" attributed by Hamilton and Zuk. Nevertheless, Hamilton and Zuk had a really good idea.

Anders Møller (1990) improved on correlational aspects of Hamilton and Zuk's comparative study by performing a careful series of manipulative experiments within a single species. Rather than collect evidence on the pattern among species, Møller tackled the processes of sexual and natural selection as they relate to female choice and parasitism. Møller investigated several key processes that must be true in order for the parasite hypothesis to be true. Møller reasoned that if the Hamilton-Zuk Hypothesis were true, then the following processes should be seen within a single species:

1. Parasites should reduce the survival of a female's young

2. Parasite resistance should be heritably transmitted across generations

3. Parasite infection should lead to a visible signal that arises during a male's ornament development

4. Females should prefer males which show an indicator ornament that establishes his clean bill of health.

In a series of experiments on barn swallows, *Hirundo rustica*, Møller found support for all four predictions.

1) Blood-sucking mites applied to offspring in some nests, caused the offspring to fledge at a smaller size. Fledging size is directly related to survival to maturity.

2) Males vary in the number of parasites at the beginning of the season. To establish that such variation is heritably transmitted to offspring, Møller carried out a cross-fostering experiment. He split the clutch that a father sired and placed it in the care of "foster parents". He then inoculated offspring in foster nests with mites to measure their resistance to mites. This procedure tests for the effect of rearing environment on the susceptibility to mite infestation in offspring (e.g., foster nest). By removing the chicks from their natural parents, the problem of a father passing on an infestation to offspring is overcome. Offspring that overcame the mite infestation were more likely to come from males that were parasite-free at the beginning of the season than were offspring that came from infested fathers.

3) Infestation during youth has an effect on ornament development at maturity. By using Pyrethrin, Møller was able to kill mites on some offspring, and these chicks developed longer tails at maturity.

4) Finally, females prefer males with long tails, which seems to indicate a parasite-free male. Thus, female swallows use the size of male's tail as an honest indicator of his ability to fight off parasites that are likely to decrease the fitness of the female's progeny.

Male Symmetry and Female Choice

In recent years researchers have been searching for other attributes of males that would indicate mate quality to choosy females. One simple trait that might be used by females is the relative symmetry in ornaments that a male presents to females. **Fluctuating asymmetry** refers to random perturbations in ornament size on one side of the body axis but not the other. Biologists hypothesize that such random perturbations reflect some kind of developmental instability. Where do such developmental problems arise? Researchers believe that asymmetry is an indication of genes that aren't working well with one another -- bad epistatic interactions (see Chapter 2). Thus, a female that mates with a male that is symmetric in their ornament may be choosing a male that has genes that are working well together compared to a very asymmetrical male.

A cut-and-paste manipulation of the male trait will readily allows for a test of female mate choice for symmetrically ornamented males. Male mollies are fish that possess and elongate sword on their tail that is a sexually selected trait. The males also have strong vertical barring on their sides. The number of bars and the relative symmetry of bars on the male's left and right flank may provide the female with an indication of his quality. You might think that a female cannot see both sides of the male's body at once. However, a male molly will swim back and forth in front of a female, and display each side of his body in an alternating fashion. The female has opportunity to view both the left side and right side. Is the female sensitive to an asymmetry in barring between the left and right sides of the male body?

Molly Morris (unpub.) carried out a female choice study on the degree of asymmetry in the barring pattern on *Xiphophorus cortesi*. To perform

the choice experiments, she used a small piece of dry ice to make males asymmetrical by bleaching the bars on one side but not the other. This is similar to having a tattoo removed in a tattoo parlor. To control for the effects of the dry ice treatment, Morris applied the dry ice to the area between bars, where no pigment is deposited. Females overwhelmingly choose males that had symmetric numbers of bars on one side of the body versus the other. It still remains to be determined whether males that have symmetric bars will transmit an advantage to the female's offspring. Similar experiments on the symmetry of male ornaments have found that females are quite choosy in swallows (Møller 1990), and the scorpion-fly *Panorpa japonica* (Thornhill 1992). However, the definite piece of evidence that choice of such males provides indirect benefits for a female's offspring quality, has proven elusive.

Figure 10. 20. Male *Xiphophorus multilineatus* possess prominent dark bars on their sides. Females prefer 'symmetric' males that have the same number of bars on the right and left (photo courtesy of Morris).
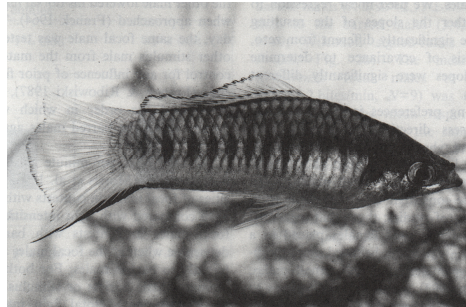
Humans and choice of the MHC locus: Genetic compatibility

A final example of choice for mate quality from a genetic perspective hits close to home. Humans appear to choose mates that are dissimilar to themselves at specific genetic loci referred to as the Major Histocompatibility Locus or MHC. As its name implies, the MHC is responsible for cell-cell recognition in the body (Bender 1991). In recognizing self, it is also possible to recognize non-self or fight off infections that take hold of the body. Greater genetic variability at MHC loci would presumably provide the body with a greater arsenal to recognize and defend against infectious diseases (see Fig. 10.24).

The MHC locus has been shown to be under mate selection that would produce high levels of heterozygosity in progeny. Recent studies on mice (Potts et al. 1991; Potts and Wakeland 1993; Potts et al. 1994) and mammals (Ober et al. 1997) have shown that both species tend to mate disassortatively in both laboratory and wild populations. Males and females select a mate that is more dissimilar at the MHC loci than would be expected under random mating. While the mechanism of mate discrimination in mice is unclear, there is evidence that humans prefer odors from individuals that differ in the alleles at the MHC locus (Wedekind and Füri 1997). Wedekind and Furi (1997) asked a group of individuals to wear a cotton shirt for 24 h. Next they asked another group of testers to sniff the T-shirts and rank the odors in terms the degree to which the shirts reminded them of their mate. By scoring the alleles at loci in sniffers and T-shirt wearers, Wedekind and Furi found that men and women who were reminded of their mate when sniffing the shirts were more dissimilar in the MHC loci of the preferred T-shirt wearer than was expected by chance. A second study characterized the MHC loci between husbands and wives in a large sample of couples. The study population consisted of American Hutterites. The married couples had a strong tendency to choose mates that were more different at the MHC-loci than would be predicted by chance alone. Taken together, humans and other mammals such as mice appear to mate disassortatively with respect to the MHC locus, presumably to enhance the fitness of their progeny by increasing the heterozygosity. The mechanism of mate choice could also provide mammals with the ability to discriminate among closely related kin from non-kin, and the MHC locus is being actively investigated for its role in kin recognition.

Figure 10.21. Full page diagram (in the works) depicting the role of MHC variability in promoting resistance to parasitic infection through the recognition of cell surface proteins (e.g., T-cells) (from (Bender 1991).

The precise proximate mechanism that is used in MHC recognition during mate choice is not currently known. It is noteworthy that some of the genes governing chemoreception and the MHC locus are closely linked in the human genome (Fan et al. 1995). Recent discoveries on human pheromones point to a potential interaction with the vomeral-nasal organ which specifically responds to the different secretions produced by males and females. The vomeral-nasal organ of humans is located in the nose, but is distinct from our sense of smell. Smells are thought of as any airborne chemical that triggers a response (aversive or

attractive). The volmeral-nasal organ (VNO) of humans is specifically responsive to pheromones such as those emitted by sweat glands, vaginal secretions, or secretions around the penis (Comfort 1971; Berliner et al. 1996). Moreover, the VNO, in response to minute quantities of specific pheromones, can trigger the release of potent gonadotropins from the brain (see Chapter 8). Gonadotropins are clearly linked to sex drive in males and females.

Cowley and Brooksbank (1991) carried out experiments using two known pheromones: androstenol that occurs in human underarm sweat, and copulin, a mixture of short-chain fatty acids, that occurs in human vaginal fluid. Each of these pheromones have been shown to promote sexual behavior in a variety of mammalian species (Melrose et al. 1971; Michael et al. 1975). While they did not address mate selection *per se*, Cowley and Brooksbanks' studies addressed the possible role of these hormones in promoting a variety of social interactions between the sexes. They constructed amulets that released the two hormones into the air, and asked that the subjects wear the amulets around their necks during a 24 h period. They also asked their subjects to make detailed entries regarding their exchanges during the same 24 h period.

Based on these experiments, the pheromones appeared to have significant effects on human behavior, but varied according to sex. In particular, females engaged in more interactions with men when they were wearing the androstenol treated amulet. No such responses were observed in men wearing the pheromone secreting amulets. The amulets containing short-chain fatty acids appeared to have no effect on either sex. The increase in female-male interactions from the adrostenol treatment suggests an interesting interplay between male pheromones, and female social contacts, which certainly warrants further study. The specific organ triggered by these pheromones is the VNO. Needless to say, the perfume industry has been putting a lot of research into the VNO of humans with the aim of making biologically based pheromones and perfumes that might be more effective than the anal gland of deer (e.g., musk) or other substances that have been used in the past.

Our study of the chemical world of female choice in humans is really in its infancy, however, we have known that such compounds have potent effects on mate attraction in diverse animal groups such as moths (Löfstedt 1993) and salamanders (Vessey 2000). Identifying which specific compounds are responsible for variation in mate choice among females, however, is a wide open field. Once specific compounds have been identified, the possibility of creating synthetic pheromonal cocktails to test mate choice has great potential.

Cognitive, Active, and Passive Female Choice

Surprisingly, little attention is given to the idea that females make cognitive choices regarding choice of mate. In contrast to the dearth of studies on female cognition, theories and empirical tests of cognition in male-male contests has received considerable attention (see Chapter 8). It is very difficult to shy away from the idea that females (or males) are somehow making active cognitive choices regarding mate quality.

Recall the three criteria for cognitive thought processes: **perception** -- a unit of information from the environment is collected and stored in memory, **data manipulation** -- several units of information that are stored in memory are analyzed according to computational rules built into the nervous system, and **forming a representation of the environment** -- a complete "picture" is formed from by processing all of the information and the organism bases its decisions on the complete picture or representation of the environment (Roitblat 1987; Real 1991).

Females of many species appear to survey and take in information about males. Are they taking in information regarding ornament size or quality? Imagine a female watching a group of males at a lek. The males possess variation in their plumage ornaments, and the female views the males in succession. Alternatively, imagine a female red-wing blackbird visiting male territories. She listens to the male's songs over the course of a few hours and then settles on a mate.

Given a choice of "n males" a female should choose the 'best of n' that she has encountered. Despite its conceptual simplicity, this problem has yet to be answered in full detail. Most of the studies discussed above only give the female the choice between two males. Females in the wild may have dozens of males vying for her attention, particularly, in areas where males aggregate, such as at a lek. Clearly, females are making cognitive choices, but how they accomplish this task is unknown. How many males should a female survey before she has the data she needs?

Figure 10.22. Janetos (1980) modeled female choice based on several possible decision making rules (listed down the right side). All models except the random rule produced a gain in fitness with increased sampling of males, but the gains after 4 or five males were small compared to the initial gains provided by just sampling two males. (from Halliday 1983, after Janetos, 1980)
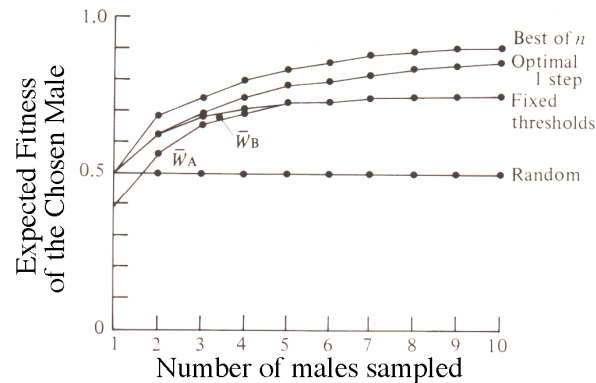
Janetos (1980) devised an early model of mate choice that is worth looking at because it makes the assumptions about mechanisms underlying choice explicit. There are three fundamental constraints on a female's behavior (Janetos 1980; Halliday 1983): time, mobility, and memory. Time and space constrain how many males a female can sample. Memory limits how much she can remember about the males when it comes time to crank through the cognitive machinery and generate a choice.

Janetos explored a number of information gathering strategies that females might use, and found that all strategies generated a curve reminiscent of the marginal gain curve of optimal foraging. After sampling only a few males, the female's success at finding the best male would rapidly level off, and searching for additional males would provide little major gains in quality of mate. A female might only have to sample 4 or 5 males before the gains in sampling begin to level off. Even simple female choices based on two males, let alone 3-5 might in fact be quite beneficial for a female. The empirical data on female choice among species (Table 10.1, next page) suggests that females are sampling roughly 2-7 males with a large number of species found around 3 males sampled.

Janetos's models suggests that a female that uses a best-of-n strategy, in which a females picks the best from a total of n males visited, appears to do better than the other mate search strategies. In particular, best-of-n

does a lot better than a fixed-threshold strategy of sampling in which a female searches for a mate until it finds one that is acceptable, or above an **absolute threshold value** for the male trait that she is using to judge male quality. However, Les Real (1990) built in more realistic search costs into the female strategies and found that the threshold strategy can actually do a better job finding a mate, if there are extensive costs to a long search. A female that finds a mate early will accept the male and avoid a lengthy search with its resultant costs. The idea of a threshold value was borrowed from an economic problem in which a company is carrying out a job search. When a suitable candidate is found that satisfies the criterion of a search the company can save a lot of money by terminating the job search (Gibson and Langen 1996). Females may gain similar benefits from a costly mate search.

Table 10.1. Number of males visited by females in a selection of species (from (Gibson and Langen 1996).

Species	Random encounter	Active Choice	Males visited
Pine engraver beetle (*Ips pini*)	yes	yes	2.8±1.5
Fiddler crab (*Uca annulipes*)	no	yes	7.5±6.0
Natterjack toad (*Bufo calamita*)	no	no	1.7±1.1
Barnacle goose (*Branta leucopsis*)	?	yes	2.4±0.6
Great snipe (*Gallinago media*)	?	yes	3.0±2.5
Sage grouse (*Centrocercus urophasianus*)	no	yes	3.7±2.6
Black grouse (*tetrao tetrix*)	no	yes	4.9±2.0
Peacock (*Pavo cristatus*)	?	yes	3.0±1.2
Cock-of-the-rock (*Rupicola rupicola*)	no	yes	3.4±2.3
Pied flycatcher (*Ficedula hypoleuca*)	?	yes	3.8±2.4
Great reed warbler (*Acrocephalus arundinaceus*)	?	yes	5.9±2.6

Despite the early introduction of Janetos' ideas and renewed theoretical interest in mate search (Real 1990; Real 1991), few researchers have undertaken experimental tests for such cognitive processes in females. Part of the success in the advancement of male cognition, was the development of experimental paradigms that allowed researchers to determine that cognitive processes really had an impact on male decision-making. The development of the neighbor-stranger recognition experiments showed that males could recognize features of neighbors, and act appropriately under situations when strangers were more of a threat than neighbors, and vice versa. Certainly individual recognition is just as important for females that pair with the same male across a number of breeding seasons (e.g., monogamous for life), as it is for a male engaged in a dear enemy relationship with a territorial neighbor across several seasons (e.g., see Chapter 8).

In addition to such recognition studies, a relatively new female choice experiment has been devised that explores a cognitive dimension in animal behavior called mate copying. **Mate copying** was originally suggested to occur in birds, particularly lekking species of birds where females were likely to encounter a large number of males in a small area (Höglund et al. 1990). The evidence from lekking species was largely observational. Females would arrive at a lek, and spend very little time making a choice. Instead they would often queue up to copulate with a single male that a number of females had already chosen to mate with.

Figure 10.23. Female copying in the black grouse, *Tetrao tetrix*, can be elicited by placing a dummy on a male's lek territory. a) Letting the male copulate with the dummy increases female visitation. b) No copying is seen if the male is not allowed to copulate with the dummy. B is the number of visits to the male the morning before the dummy is placed out, E is visits with the dummy present, and A is visits the morning after the dummy was removed (Höglund and Alatalo 1995).
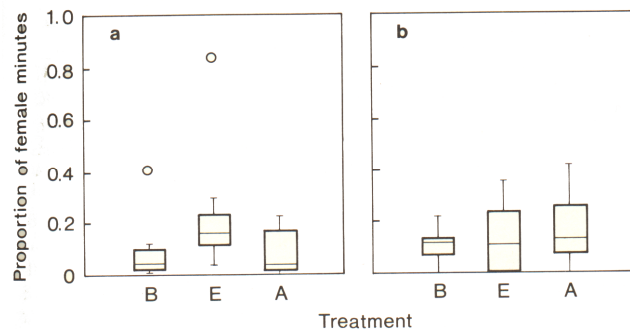
This idea received an explicit test when Höglund and colleagues (Höglund and Alatalo 1995) presented lekking male black grouse, *Tetrao tetrix*, with female dummies. Simply placing a dummy on a male's lek territory was not sufficient to elevate the number of visits he received from other females copying the dummy's placement. Rather, if the male was allowed to copulate with dummy, he experienced an increase in female visitations.

Instead of grappling with a myriad of choices, young females might copy the choices made by older females. An older female, might already have an idea of a male's genetic quality because she has bred with him in the past and successfully reared offspring. Mate copying might be adaptive when sampling lots of males is a relatively costly proposition. The phenomenon of mate copying adds a potentially important cognitive component to the study of mate choice. How can we perform experiments that prove females make cognitively-based choices.

The best experimental demonstration of mate copying is found in the guppy, *Poecilia reticulata* (Dugatkin and Godin 1992). Dugatkin devised a testing procedure that clearly demonstrates copying behavior. Dugatkin gave females a choice between two males. He them removed the female to an area where she watched a second interaction between the male that she rejected on the first trial and the male she preferred. Dugatkin used a 'dummy female' to simulate a female showing preference for the male that she rejected, while the male she preferred was observed without a female. Dugatkin then repeated the original pairing of the two males with the female, and found that females showed a significant shift in preference toward the previously unpreferred male. The effect of such 'copying behavior' can be so strong that it can even override genetically based preferences that females have for males that vary in the amount of orange coloration.

Mate copying experiments still have to be devised in natural settings to determine the importance of copying in the wild. In addition, the precise adaptive value of such mate choice remains to be determined. What kind of benefit is the female getting? Is she avoiding the costs of searching for a mate, or is she using information acquired by more experienced females? Mate copying is only a single dimension of the possible cognitive processes that are undoubtedly involved in mate choice. Many

more experiments need to be devised to test other cognitive processing. Nevertheless, mate copying can generate a powerful positive frequency dependent selection that can destabilize negative frequency dependent selection that preserves variation among male morphs (Chapter 9).

The example of mate copying is a clear example of a kind of **active female choice**. Such cognitive models of mate choice are clearly distinct from models of **passive female choice**, such as those involved in sensory bias. The idea of **indirect female choice** arises from the observation that many females engage in some sort of pursuit ritual during courtship. Female butterflies often flee the advances of amorous males. Females are not necessarily actively making choices during such courtship ritual, but through the female's actions, they are causing selection on a male's traits. Many courtship routines entail elaborate and vigorous chasing, and a female may indirectly select the best male to perform such actions. Only the fittest male can keep up with her and stragglers will be weeded out. Selection favors the more vigorous and ardorous males and any aspects of secondary sexual traits that aid in such pursuit or once caught, aid in clasping (e.g., amplexus) (Shuster and Wade 2004).

Summary: Adaptation of Choice in Advertising

The fundamental selective pressure that causes mate choice to evolve in one sex and ornaments to evolve in the other is related to how much energy each sex contributes to young. The sex with the lower investment in young is freer to search for a large number of mates, while the sex with a high investment is removed from the pool of breeding adults and usually has less mating opportunities. This ecological constraint causes a bias in the operational sex ratio that favors choice in the sex with greater reproductive investment. The sex with low investment evolves armaments for male-male competition (e.g., see Chapter 9) or ornaments that serve to attract.

In most species, females provide energy to young. However, males provide extensive care or energy in a few sex-role reversed species. In some of these species, females develop ornaments. As predicted by theory, manipulations of operational sex ratio in sex-role reversed pipefish and Mormon crickets alters the degree of mate choice, or even the sex that expresses mate choice. Male pipefish prefer large females when females are abundant, but mate randomly as a function of size if males are abundant. Likewise, Mormon cricket males prefer large females when the nuptial gift (spermatophore packet) they provide is a scarce commodity. Under food limitation males can only make a single spermatophore packet and mate with one female, while at the same time females attempt to mate with several males. Conversely, Mormon cricket females are choosier when males have abundant resources for production of many nuptial gifts. Nuptial gifts are examples of direct selection on female choice because the female receives a direct benefit in terms of energy that enhances reproduction. In many species, males provide resources to the females in the form of a high quality territory and females often prefer males on the basis of the male's extended phenotype or his territory quality. Manipulations of male ornaments, and the male territory are essential to disentangle the cause and effect criteria that underlie mate choice.

Males of many species provide no gift, no territory, and no apparent resources that the female can use for directly enhancing her fitness. In such cases, the existence of male ornaments is somewhat of a puzzle. Why should a female choose a highly ornamented male if she receives no benefit from her choice? The enormous exaggeration of ornaments is likewise a puzzle given that many ornaments result in a fitness cost to the male (e.g., predation in guppies). Two theories of mate choice consider the indirect selection that acts on female choice through sexual ornaments in the male. Both theories are somewhat unusual because the evolution of adaptations that are used by the female for choice become coupled to adaptations used by the male for attraction.

The first theory, runaway Fisherian sexual selection assumes no indirect benefit to females, but rather, choosy females end up picking mates they naturally find attractive, which leads to strong assortative mating. Moreover, genes for female choice and the genes for the male trait get bundled together in their progeny as a potent genetic correlation. Because ornamented males acquire more females than non-ornamented males the ornamented males have higher fitness. Alleles for female choice hitchhike a ride on the high fitness of sexy males and both male ornaments and female choice can increase to absurd levels of exaggeration in a population. The assortative mating can drive a self-reinforcing runaway process.

The second theory, good genes, also posits that a genetic correlation gets formed by virtue of genes expressed by choosy females for ornamented males. However, good genes models also assume the existence of a third class of genetic loci, the good genes that females are choosing when they pick a male with a large ornament. Because ornamented males bear a survival cost to begin with, those ornamented males that also carry good genes are more likely to survive to maturity than ornamented males that carry poor genes. Males without ornaments do not bear a tremendous survival cost to maturity and they are just as likely to possess good genes or lack them. Males with small ornaments may also develop small ornaments because they lack good genes. Accordingly, a female that picks a male with a large ornament is much more likely to acquire good genes for her offspring thereby gaining an indirect benefit.

Discerning between runaway versus good genes models of sexual selection cannot be accomplished by measuring a genetic correlation between female choice and the male ornament, nor can it rely on the existence of survival costs to the male ornament; both models assume their existence. The genetic correlation is present in many species with sexually selected ornaments, as are survival costs in males. The runaway model assumes less about the process of sexual selection than the good genes models. It is more similar to a *null model* of sexual selection. Good genes are considered a more complex *alternative model* that requires additional empirical support; males with large ornaments produce quality offspring. Evidence is accumulating that male ornaments are linked to genes that enhance progeny such as parasite resistance (e.g., swallows), growth, and survival (e.g., peacocks).

Cognitive models of mate choice are clearly distinct from models of **passive female choice**, such as those involved in sensory bias, the subject of upcoming Chapters (13, 19). A large amount of work remains to be carried out on cognitive processes involved in female choice. Mate copying is perhaps an example of cognitive or active female choice, in which females sample a selection of males or alternatively opt to mate with males based upon information other females have collected on the quality of a male. Additional data must be collected to determine whether mate search and copying by females satisfies criteria of cognitive processing. The experimental paradigm of mate copying may allow for rapid progress to be made on cognitive aspects of mate choice.

Study Questions for Mate Choice

1. Why do females choose and males display (in most animals)?

2. What is the male's extended phenotype, and give an example of an experimental test of the role of the male's extended phenotype in affecting female choice. Why is it necessary to do such experiments?

3. What are two assumptions of the model of runaway process? What is a key prediction of the theory of sexual selection by runaway process? Describe evidence supporting the key prediction.

4. How do these two assumptions differ from indicator models of female choice?

5. Describe why a comparative test of the parasite/sexual selection hypothesis that compares different species is less powerful than an experimental test within a single species?

6. Do females forage for mates?

7. Define direct versus indirect benefits of mate choice. Give an example of each (or one example with both).

8. Why should you avoid using cologne or perfume if you are searching for the true love of your life?

9. What is female copying?

10. Outline the null hypotheses, and alternative hypotheses for all the relevant models of mate choice.