PSYCH 3T03 Midterm 1 Textbook Readings

Chapter 1: An Evolutionary Approach to Animal Behaviour

I. Understanding Monogamy

Male prairie voles are capable of monogamy unlike most other mammalian species, including many other voles. The *ventral pallidum* contains many cells with V1a receptor proteins that bind to the hormone vasopressin. When V1a receptors are stimulated by vasopressin upon copulation with a given female, neural pathways are triggered that provide positive feedback, leading to the formation of a durable social attachment. V1a receptors are less numerous in the ventral pallidum of polygynous vole species.

By increasing the number of brain cells in the ventral pallidum with an active form of *avpr1a*, the gene encoding V1a receptors, researchers were able to boost the tendency of male prairie voles (and later, male meadow voles) to remain close to a social partner (even if they had not mated with them). The prairie vole's *avpr1a* gene has a section of DNA that is lacking in the polygynous vole's gene, which might increase the abundance of V1a receptors in the ventral pallidum and contribute to the monogamous behaviour of male prairie voles.

Others argue that a male that bonds with one mate is reproductively successful because he can keep his female partner from copulating with other males, particularly in low-density populations where it may be difficult to find another available mate. If mate-guarding males in the past tended to have more surviving descendants than males that behaved in other ways, then those monogamous individuals would have shaped the evolutionary history of their species.

Employing an evolutionary perspective, monogamy in prairie voles may be the product of a series of behavioural shifts, with polygyny leading to infanticide, which may have favoured females that tended to mate with several males to keep them confused about the paternity of their young. But female promiscuity could have then favoured any male that guarded a single mate and even cared for the offspring she produced, leading to the kind of monogamy exhibited by today's prairie voles.

Proximate and Ultimate Explanations in Biology: *Proximate* explanations about behaviour deal with what is responsible for the development and operation of an animal that enables it to behave in a particular way, e.g. heredity, development of sensory-motor systems via gene-environment interactions, nervous system detection of environmental stimuli, hormonal response to environmental stimuli, skeletal muscles. Alternatively, *ultimate* explanations involve events that happened in previous generations, e.g. events occurring over evolution from the origin of the trait to the present; past and current usefulness of the behaviour promoting a lifetime of reproductive success.

The four main questions for behavioural researchers according to Niko Tinbergen:

1. How does an animal use its sensory and motor abilities to activate and modify its behavioural patterns?
2. How does an animal's behaviour change during its growth, especially in response to the experience that it has while maturing?
3. How does the behaviour promote an animal's ability to survive and reproduce?
4. How does an animal's behaviour compare with that of other closely related species, and what does this tell us about the origins of its behaviour and the changes that have occurred during the history of the species?

II. Darwinian theory and Ultimate Hypotheses

Darwinian theory is based on the premise that evolutionary change is inevitable if just three conditions are met: (1) **Variation**, such that members of a species differ in some of their characteristics, (2) **heredity**, with parents able to pass on some of their distinctive characteristics to their offspring, and (3) **differences in reproductive success**, such that some individuals have more surviving offspring than others in their population as a result of their distinctive characteristics. **Natural selection** – if hereditary variation exists within a species and if some hereditary variants consistently reproduce more successfully than others, the population will evolve, becoming increasingly dominated by the reproductively successful type. Genetic variation occurs when a given gene exists in two or more forms, or **alleles**.

Darwinian Theory and the Study of Behaviour: **Artificial selection** causes evolutionary change as predicted by the theory of natural selection; an experimenter only permitted mice that collected large amounts of cotton for their nests to breed with each other, which led to the evolution of populations (the high lines) whose members collected much more cotton on average than controls, whose behaviour was not selected and so did not evolve. Likewise, selective breeding of mice that gathered relatively little cotton resulted in the evolution of low lines, whose members made very small nests. Although children everywhere can digest lactose, most lose this ability when they are no longer being nursed. Once dairying originated in northern Europe, a mutant gene spread naturally through the population that contributed to the ability of adults to digest milk sugar.

The Problem with Group Selection: **Group selection theory** – According to Wynne-Edwards, species that had self-sacrificing individuals would be able to keep their numbers down and their essential resource bases intact. This was challenged by Williams who showed that survival of alternative alleles was much more likely to be determined by differences in the reproductive success of genetically different individuals than by survival difference among genetically different groups. For example, imagine there were male langurs prepared to risk serious injury or death by killing infants in order to regulate their band's size for the survival benefit of the group; group selection would favour the alleles for male infanticide because the group as a whole would benefit from the removal of excess infants. However, provided there were two genetically different males at any time, ones that practiced infanticide for the good of the group and the other that permitted other males to pay the price for population reduction, non-killers would typically have greater reproductive success. Hereditary material of infanticidal males would thus decrease in frequency over time. Therefore, although group selection can occur, if it favours a trait that involves reproductive self-sacrifice while natural selection acts against it, the latter seems likely to have a stronger evolutionary effect.

PSYCH 3T03 Midterm 1 Textbook Readings

Testing Alternative Hypotheses: If high population density really does cause male langurs to behave abnormally (social pathology hypothesis) or if it threatens the survival of langur groups, thus activating infanticide by self-sacrificing males (population regulation hypothesis), then we would expect to see infanticide by males only in areas where langurs live in exceptionally high density (proven false). If males kill infants after taking over a band of females in order to replenish energy reserves that have been depleted in the takeover struggle (cannibalism hypothesis), we would expect male langurs to consume the infants they kill (proven false). Applying the quicker reproduction hypothesis, we would expect males to avoid eating their own babies (proven true) and females who have lost an infant to a killer male to promptly resume sexual cycling (suppressed when nursing young) and to become receptive to that same male (proven true).

In lion species, new males sometimes oust previous pride masters and often succeed in killing youngsters less than 9 months old. Once a lioness has lost her cubs, she will resume sexual cycling and mate with her infanticidal companion. Had she retained her infant, she would not have become sexually receptive until her progeny were two years old. Since the average tenure of an adult male with a pride of females is only 2 years, the reproductive benefits of infanticide for the male lion after a takeover are obvious. Similarly, in species in which females compete for sexual access to males, e.g. giant water bug, jacana (water bird), we see the evolved capacity among females for infanticide.

Certainty and Science: Although the meadow vole and a close relative do not have the special sequence of bases found in the prairie vole's *apr1a* promoter region, it has been shown that many other thoroughly polygynous voles and other polygynous mammals do. Given the conflicting data, it is appropriate to be cautious regarding the one-gene hypothesis for vole monogamy.

<u>Chapter 2: Understanding the Proximate and Ultimate Cases of Bird Song</u>

I. Different Songs – Proximate Causes

In one study that tested the genetic difference hypothesis, researchers found little genetic differentiation among six different dialect groups of white-crowned sparrows. Song learning hypothesis based on laboratory experiments with white-crowned sparrows – according to this hypothesis, young white-crowns have a critical period 10 to 50 days after hatching, when their neural systems can acquire information from listening to white crown song, but not to any other species' song. Later in life, the bird matches its own sub-song with its memory of the tutor's song and eventually imitates it perfectly, unless it is deafened after hearing others sing but before beginning to vocalize itself. The ability to hear oneself sing appears to be critical for the development of a complete song in a host of songbirds.

Social Experience and Song Development: A problem with these classic experiments by Marler was that birds were reared in environments that lacked opportunity for social interaction. To test whether social stimuli can influence song learning in white-crowns, researchers placed young white-crowns in cages where they could see and hear living adult song sparrows or strawberry finches. Under these circumstances, white-crowns learned their social tutor's song, even when they could hear, but not see, adult male white-crowned sparrows. In fact, social experience with another species can trump early tape tutor experience with white-crown song even after the young males are 50 days old, the end of the window of opportunity for social learning from tape tutors. In nature, young starlings (who are adept at mimicking human speech when hand-reared in a human household) and white-crowned sparrows are strongly stimulated by interactions with vocalizing companions of their own species. The same holds true for song sparrows, among whom the social effect is stronger when birds are 8 as opposed to 2 months old, as well as when song is overheard through indirect observation between two or more adults.

The Development of the Underlying Mechanisms of Singing Behaviour: Males have two Z chromosomes, whereas females have a Z and a W chromosome, the latter having fewer genes. These genetic differences have large effects on embryonic development; gonadal cells give rise to testes and ovaries in males and females, respectively. Cells in the young testes, unlike in the ovaries, secrete testosterone, which interacts with testosterone-sensitive receptors. This results in the growth of specialized neural circuits that will eventually be used in singing males. The differences in male and female brains are the product of both genetic and environmental (i.e. cellular chemical products or preceding gene-environment interactions) differences. Cells in male bird brains convert testosterone into estrogen; this self-manufactured environmental signal activates the development of specific neural pathways found in the male's brain. These circuits link the elaborate network of neural structures, known as the song control system, whose integrated operation is required for song. Normally, certain clusters of brain cells that grow rapidly in size in young male zebra finches shrink over time in young females. In immature females subjected to estrogen treatment, these song control units increase in size, providing support for the hypothesis that a critical chromosomal-hormonal connection sets off a series of gene-environment interactions underlying the development of a male song control system in a zebra finch's brain.

When a young bird is bombarded with sounds produced by singing adults of its own species, these sounds activate special sensory signals that get relayed to particular parts of the brain. In response to these distinctive inputs, some cells in these locations alter their biochemistry (i.e. changes in gene expression) in order to change the bird's behaviour. As zebra finches attempt to match a tutor's song, the activity of a gene called *ZENK* rapidly increases in certain song control neurons, resulting in corresponding increases in cellular amounts of the protein encoded by that gene. This protein is believed to be involved with subsequent alterations of these neural circuits, causing them to become highly selective in responding to the individual's own song as opposed to any other. As the finch gains a crystallized full song, further changes in cell architecture or biochemistry in its song control system cannot improve its ability to sing that song, and *ZENK* activity therefore shuts down. In a similar study, *FoxP2* was inhibited in experimental males, who subsequently failed to imitate the songs they heard from a tutor finch as well as control males.

How the Avian Song Control System Works: Neural pathways carry signals from the higher vocal center (HVC) to the robust nucleus of the arcopallium (RA) to the tracheosyringeal portion of the hypoglossal nucleus (nXIIts) to the muscles of the song-producing syrinx. Other pathways connect the nuclei, such as the lateral portion of the magnocellular nucleus of the anterior nidopallium (lMAN) and area X, that are involved in song learning rater than song production. The importance of the RA in song production is demonstrated in studies showing that the male RA is much larger than that of females; similarly the importance of lMAN for song learning is demonstrated by the reduced or absent lMAN nuclei in bird species that do not learn their songs. In general, male song repertoire is correlated with HVC size. Studies that have assessed whether the HVC must be large for a bird to learn or whether learning makes the HVC expand in response to stimulation have shown that in both warbler and wren species, the male brain develops largely independently of the learning experience of its owner; this suggests that the production of a large HVC is required for learning, rather than the other way around. By recording the responses of single cells in a swamp sparrow's HVC to playbacks of that bird's own songs, researchers discovered a number of HVC relay neurons that generated intense volleys of action potentials upon exposure to one song type only. So here we have a special kind of cell that could help the sparrow identify which song type it is hearing, the better to select the best response for a particular situation.

II. Different Songs – Ultimate Causes

Song learning occurs in members of just 3 of the 23 avian orders: parrots, hummingbirds, and songbirds. Members of the remaining 20 orders of birds produce complex vocalizations, but they do not have to learn how to do so, as shown in experiments wherein young birds that were never permitted to hear a song tutor, or were deafened early in life prior to the onset of song practice, nevertheless came to sing normally. If we assume that the long-extinct bird that gave rise to all modern species did not learn elements of its songs but instead produced vocalizations instinctively, as do many modern bird groups, then song learning must have evolved independently in three different lineages of modern birds. On the other hand, song learning may have originated in a common ancestor of parrots (Psittaciformes), hummingbirds (Trochiliformes), and passerine songbirds (Passeriformes), and may have been retained in these three lineages while being lost in other descendents of that ancestral song-learning species. The first scenario is more parsimonious since it requires three as opposed to four evolutionary innovations, and is therefore considered somewhat more likely to have occurred. However, by capturing birds that have just been singing and killing them immediately, researchers have shown that the *ZENK* activity maps of the brains of selected parrots, hummingbirds, and songbirds reveal strong similarities in the number and organization of discrete centers devoted to song production and processing, e.g. the caudomedial neostriatum (NCM), located in roughly the same part of the brain in all three groups, shows *ZENK* activity when individuals are exposed to the songs of others. These similarities would seem to rule against the hypothesis that song-learning abilities evolved independently in the three groups of birds.

The Reproductive Benefits of Song Learning: Vocalization conveys information about species membership; by broadcasting a clear message that a particular site or a particular female is defended by a physiologically fit singer, a male might deter conspecific competitors looking to steal territory or mates; territories from which resident male white-throated sparrows were experimentally removed attracted fewer intruders when the taped song of the removed male was broadcast from his vacant territory; male singers able to communicate their species identity to females might attract mates more readily than those whose songs are less distinctive; females that rapidly locate males of their species can begin reproducing sooner and avoid the risks of mating with members of another species; the mate attraction hypothesis for song distinctiveness correctly predicts that females will respond to taped songs of their own species more strongly than to those of other species

The Benefit of Learning a Dialect: (1) Ability of a young male to fine-tune his song so that it resembled the songs of other individuals in a particular region; certain dialects are transmitted with unusual effectiveness in certain habitats, i.e. high-frequency sounds become less degraded in open habitats than in places with thick foliage, where lower frequencies are more suitable; (2) advantages of matching songs to the singer's social environment; a mutual non-aggressive pact based on learned song signals could benefit both an established resident and a rival newcomer by helping them conserve time and energy; this hypothesis correctly predicts that some male species can change their crystallized full songs in order to more closely match the songs of neighbours in a new territory. The fact that song sparrows type-match and repertoire-match so often indicates that they recognize their neighbours and know what songs they sing and that they use this information to shape their replies. Their choice may enable them to send graded threat signals. Song sparrow males can control the level of conflict with a neighbour by their selection of songs. When a foal male sings a shared song at a rival, the neighbour has three options: one that will escalate the contest (type-match), keeps it at the same level (repertoire match), or de-escalates the interaction. Likewise, the initiator of the contest can select a matching song type, repertoire match, or an unshared song type.

If this ability to modulate song challenges is truly adaptive, then we can predict that male territorial success, i.e. territorial tenure, should be a function of the number of songs types that a male shares with his neighbours, while species in which territorial males come and go quickly should not exhibit song learning and sharing between neighbours, but rather, song characteristics of their species as a whole to facilitate communication with all conspecifics.

Female Preferences and Song Learning: In a species that is divided into stable subpopulations, males are likely to have genes passed down from successful ancestors; therefore, by learning to sing the local dialect, males could announce their possession of traits and genes well adapted for that particular environment. Females might gain by having preference for males that sing the local dialect because they would endow their offspring with genetic information that promotes the development of locally adapted characteristics. However, if males can change their dialect from territory to territory, then females cannot rely on this trait to identify his birthplace.

Females might also use song repertoire as an indicator of a male's genetic quality, immune function, or condition; a healthier partner might be able to provide his offspring with above-average parental care (negative effects on early nutritional stress on brain development and HVC volume). The quality of vocal learning could give female songbirds a valuable clue about the quality of the singers as potential mates; song learning occurs when males are very young and growing rapidly. If rapid growth is difficult to sustain, then young males that are handicapped by genetic defects or nutritional stress should be unable to keep up, resulting in suboptimal brain development. A study that assessed the mean number of pre-copulatory displays given by female song sparrows in response to playback of the songs of males that had been able to copy their tutor songs very accurately and of males of lower copying skill showed that the more accurately copied songs elicited significantly more displays from the females. Similarly, female zebra finches preferred to fly to and perch near speakers from which were broadcast songs of non-stressed as opposed to stressed males. Additionally, females spent more time next to the speaker playing the direct song type of either an unfamiliar male or her mate compared with the speaker playing her mate's slower, more variable (undirected) song.

Chapter 10: The Evolution of Reproductive Behaviour

PSYCH 3T03 Midterm 1 Textbook Readings

I. The Evolution of Differences in Sex Roles

The bowerbird is one of 20 species in the bowerbird family, 17 of which build bowers. No other bird species builds anything like these elaborate display structures, and so the trait appears to have evolved just once. If so, a single common ancestor of the modern bowerbirds gave rise to the cluster of bower-building species, from which derived two groups of modern bower-building species, the avenue (including the satin bowerbird and maypole bowerbirds. If the mate quality advertisement hypothesis is correct, then attractive, well-decorated bowers should be built by males that are superior in some way to those birds that cannot erect a top-notch bower. Males that build better bowers have fewer parasitic feather mites than those that make less appealing display structures. The bower's quality is also an indication of the developmental history and brain size of the male. Because most females mate with just one male, male reproductive success is variable.

Small sperm usually vastly outnumber the larger eggs available for fertilization in any population, setting the stage for competition among males to fertilize those eggs. Expenditures of time, energy, and risks taken by a parent to help one offspring are considered **parental investment** in that offspring if they reduce the chance that the parent will reproduce successfully in the future. Key behavioural differences in parental investment have apparently evolved in response to the difference in the size and number of gametes.

Testing the Evolutionary Theory of Sex Differences: Sex role reversal occurs in the mating swarms of certain empid flies, in which the operational sex ratio is heavily biased because most males are off hunting for insect prey to bring back to the swarm. When a male enter bearing his nuptial gift, he gets to choose from among many ornamented partners available to him. Male Mormon crickets transfer to their partners an enormous edible spermatophore, which constitutes 25% of the male's body mass and therefore permits him to mate only once. Females are able to produce several clutches of eggs and persuade males to mate with them. Female katydids compete to mate with males that supply them with nutritious spermatophores, however when food availability is no longer scare and pollen-rich grass trees are the predominant food source, the OSR becomes male-biased because egg production is limited by the speed at which females can turn pollen into gametes.

II. Sexual Selection and Competition for Mates

Darwin defined sexual selection as "the advantage that certain individuals have over others of the same sex and species, in exclusive relation to reproduction." Although males of many species battle for females, in other species conflicts among males have to do with their standing in a dominance hierarchy. If the costly effort to achieve high status in a dominance hierarchy is adaptive, then high-ranking individuals should be rewarded reproductively. In savanna baboons, male dominance is always positively correlated with male copulatory success with fertile females. Microsatellite analysis of infants reveals that a male's dominance also predicts his genetic success.

Alternative Mating Tactics: Socially subordinate baboons can compensate for their inability to physically dominate others by developing friendships with females. In demonstrating his willingness to protect her and her offspring, the female may seek him out when she enters estrus again. Male baboons also form alliances with other males in order to collectively confront a stronger rival that has acquired a partner, forcing him to give her up.

When small iguanas run to mount a female, a larger male may remove him without effort. Because it takes 3 minutes for a male iguana to ejaculate, smaller males ejaculate prior to copulation and store the sperm in their bodies. In this way, the smaller iguana can pass viable sperm to his mate even if interrupted by a dominant male.

Conditional Mating Strategies: In a species with conditional strategies, the ability of disadvantaged individuals to switch to an alternative tactic yields a higher payoff than if these individuals were to use the tactics of their dominant opponents. In the Panorpa scorpionfly, (1) some males aggressively defend dead insects, a food resource highly attractive to receptive females, (2) other males secrete saliva on leaves and wait for occasional females to come and consume this nutritional gift, and (3) others grab females and force them to copulate. A male Panorpa can adopt whichever of the three tactics gives him the highest possible chance of mating, given his current competitive status. This is in favour of the conditional strategy hypothesis, which states that differences between behavioural phenotypes are environmentally caused, rather than based on hereditary differences.

Distinct Mating Strategies: There are three different forms of the sponge isopod; the large alpha male, the female-sized beta male, and the tiny gamma male. Each type uses a different hereditary strategy; we know this because (1) the differences between males are hereditary, and (2) the mean reproductive success of the three types is equal. If the three tactics had resulted from the same conditional strategy, then (1) the behavioural differences between them should be induced by different environmental conditions, and (2) the mean reproductive success of males need not be equal.

Sperm Competition: Male black-winged damselflies defend territories in which females lay their eggs and may mate with multiple males at different sites. A male physically removes between 90 to 100 percent of rival sperm from their mate's sperm storage organ before transferring their own. Sperm competition has shaped the evolution of the black-winged damselfly's penis, which has lateral horns and spines that enable him to scrub out a female's sperm storage organ before passing his own sperm to her.

The reproductive anatomy of fertilization in birds: when a mature ovum produced in an ovary is released it travels down the oviduct, where is may encounter sperm and become fertilized. Viable sperm received from males can be stored for lengthy periods in small tubules, especially in the interior wall of the uterus. The sperm gradually move out of the tubules over time and migrate up the oviduct to meet freshly released eggs. After fertilization, the hard tubular shell is added in the uterus before the egg is laid via the cloaca. When female collared flycatchers are experimentally prevented from receiving sperm from their social partners, some do not copulate with another male and the number of sperm available for fertilizing eggs falls over time. However some other females do have an extra-pair mating in the middle or late part of the mating period. Under natural conditions, a female flycatcher could use her control of copulations to manipulate the number of sperm from different males within her reproductive tract.

Mate Guarding: The male orb-weaving spider dies within minutes after having inserted both pedipalps into a female's paired genital openings. After insertion, the tips of the pedipalps inflate to promote insemination and block entry to the female's sperm-receiving apparatus. The most common tactic is, however, to simply stay with a mate. In general, the benefits of mate guarding increase with the probability that unguarded females will mate again and use the sperm of later partners to fertilize their eggs. A study with Seychelles warblers showed that by tricking males into ending their guarding prematurely by placing a false warbler "egg" in a nest a few days before the male's partner was due, males used the cue of egg presence to stop mate guarding at a time when their partner was still fertile. As a result, many of the unguarded females copulated with neighbouring males and used the sperm to fertilize their eggs. Because mate guarding is costly, we can also predict that males will adjust their investment in mate guarding in relation to the risk of cuckoldry.

III. Sexual Selection and Mate Choice

Male redback spiders often make it easy for their mates to eat them. Once eaten, the deceased male does in fact derive substantial benefits; the intensity of predation on wandering male redbacks is such that fewer than 20 percent manage to locate even one mate, suggesting that the odds that a male could find a second partner if he should survive his initial mating are exceedingly low. Moreover, when a male redback is finished transferring sperm, he may break off the tip of his sperm appendage in the female's reproductive tract, reducing the chance that another male can mate with her. In this situation, the mutilated male has little or no residual fertility and therefore needs very little benefit from sexual suicide in order to make the trait an adaptive one.

Mate Choice without Material Benefits: Good parent theory explains aspects of male colour, ornamentation, and courtship behaviour as sexually selected indicators of a male's capacity to provide parental care. Despite the fact that male canaries do not help rear their young, a female canary's choice of mate is heavily influenced by his ability to rapidly sing a certain, broad-bandwidth portion of the male song, the A phrase, which is composed of two note syllables, i.e. the outer edge of male song capacity. Females that hear this trill readily adopt the pre-copulatory position and may additionally reward males by adding testosterone to the eggs fertilized by their sperm. This is a maternal investment that other birds also make when mated by attractive males and one that enhances the chance of optimal development.

Does Male Courtship Signal Male Quality? According to the **healthy mates theory**, female preferences are focused on a potential sexual partner's health or parasite load as indicated by his courtship displays and appearance. The **good genes theory** proposes that preferences for certain male ornaments and courtship displays enable females to choose partners whose genes will help their offspring develop physiological mechanisms to combat infection and disease. Good genes derived from males could also be involved in identifying high levels of heterozygosity. As such, these selective females would help their offspring avoid the developmental problems associated with inbreeding.

The **runaway selection theory** argues that discriminating females acquire sperm with genes whose primary effect is to influence their daughters to prefer the male traits their mothers found attractive and to endow their sons with attributes that will be preferred by most females, even if those traits actually reduce the survival chances of individuals that possess them. Imagine that a slight majority of the females in an ancestral population had a preference for a certain male characteristic; females that mated with preferred males would have produced offspring that inherited the mate preference genes from their mothers and trait genes from their fathers. Sons that expressed the preferred trait would have enjoyed higher fitness because they would possess the key cues that females find attractive. Daughters that responded positively to those cues would have gained by producing sexy sons with the trait that many females liked. Thus, female mate choice genes and preferred male attribute genes could be inherited together. This pattern could generate a runaway process in which ever more extreme female preferences and male attributes spread together as new mutations affecting these traits occurred. The runaway process would end only when natural selection against costly or risky male traits balanced sexual selection in favour of traits that appealed to females. Any preexisting preference of females for certain traits could conceivably get the process under way; not necessarily traits that improve survival, feeding, etc. As a result, traits opposed by natural selection because they reduced viability could still spread through the population on the basis of female preference.

Testing the Health Mate, Good Genes, and Runaway Selection Theories: not mutually exclusive; for example, males in superb physiological condition, to uphold such elaborate traits/displays, would probably have to be highly effective foragers (good genes) as well as parasite-free (health), in which case females mating with such males would be unlikely to acquire parasites and their daughters would inherit survival-benefitting genes, while their sons received the pure attractiveness genes of the father.