

**Why Peahens Mate with Handicapped Peacocks  
and Why Ugly Birds Lek with Them**

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Biology 416 – Evolution

## Introduction

If natural selection is the mechanism by which phenotypes evolve, how could the ungainly, though beautiful, tail of the Indian peacock (*Pavo cristatus*) have evolved? What is the evolutionary mechanism that allows this seemingly non-adaptive character to persist in wild populations? More than two hundred years ago, questions about such an extravagant secondary sexual character puzzled the mind of Charles Darwin, leading him to develop the theory of sexual selection in 1871 (Moller & Pomiankowski, 1993). Darwin's explanation survived with little supporting evidence until very recently, in the early 1990s, when groundbreaking research began to unveil possible mechanisms to support his rough, yet insightful, explanation of the peacock's tail (Alcock, 2005, p. 372; Gadagkar, 2003).

Furthermore, if all organisms behave in such a way as to maximize their reproductive success in order to pass their genes on to the next generation, why do species like the peacock form mating enclaves called leks? What do weak and unattractive males, overshadowed by the grandeur of their more well-endowed neighbours, have to gain from clustering around them during the mating season? Compounding the problem presented by evolutionarily expensive secondary sexual characters, the conundrum of this species' lekking behaviour has perplexed the scientific community.

Devising theories to explain the evolutionary processes that lead to both ornate secondary sexual characters and seemingly backward courtship behaviours are topics of heated debate in current evolutionary research. Unresolved, these puzzling observations, which contradict the generally accepted view of evolution by natural selection, stand as road blocks to the advancement of evolutionary theory. Since evolution is one of the most elegantly unifying themes in the study of the natural world, discovering answers for these quandaries is essential for maintaining the vitality of biological intrigue. Moreover, these complex investigations that are, admittedly, not well-understood are balanced on the edge of one of the most controversial, and potentially Copernican, topics in biology: behavioural evolution. Comprehending the reasons for the evolution of animal, and consequently human, behaviours has serious philosophical, ethical and socio-political implications that hardly reside within the borders of scientific research, as workers begin to dabble in territory not entirely their own.

The evolution of behaviour leaves behind no fossil record and the genetic basis for behavioural characters is only beginning to be expounded; therefore, it is with great temerity that science should move forward as it seeks to find truth in these areas that are difficult to study empirically. Hypotheses must be weighed critically in light of the many assumptions that must be made in order to formulate models of behavioural evolution. This review endeavours to articulate the best supported hypotheses of sexual selection for elaborate tails and lekking behaviour in peacocks. Respectively, it presents the handicap principle and kin selection as the predominant mechanisms by which the peacock evolved its showy tail and strange lekking behaviour.

## **Sexual Reproduction, Dimorphism and Selection**

Sexual reproduction is the beginning of any discussion on sexual selection as a means of evolution. It is “[s]exual reproduction [that] creates a social environment of conflict and competition among individuals as each strives to maximize its genetic contribution to subsequent generations” (Alcock, 2005, p. 373). Asexual reproduction is a less complicated scenario by far since sex adds more extensive evolutionary demands, requiring organisms to not only survive, but to find a mate and somehow get it to cooperate for long enough to procreate (Freeman & Herron, 2004, p. 375).

Sexual selection for a particular individual of a species is when it has greater reproductive success than others of the same population because of the relative dominance of its reproductive phenotype in that particular environment (Freeman & Herron, 2004, p. 275). More precisely, sexual selection acts on the variation in individuals’ ability to obtain mates and produce offspring. Over generations, sexual selection results in an increase in the prevalence of characters that make it easier for an individual to copulate and raise young (Freeman & Herron, 2004, p. 376). As with natural selection, sexual selection acts in three characteristic manners: as a stabilizing force that maintains a character, a disruptive force that leads to the development of two different characters, and a directional force that causes a shift from one character to another (Hosken & Stockley, 2004). Directional sexual selection is best supported as the means by which the peacock’s tail, among other complex secondary sexual displays, evolved (Hosken & Stockley, 2004).

Sexual dimorphism (i.e., when there is a morphological/behavioural difference between the two sexes of a species) is a prerequisite for directional selection, which allows for the evolution of such characters as the peacock’s tail (Freeman & Herron, 2004, p. 374). The evolution of sexual dimorphism relies on a difference between the forces of sexual selection acting upon each sex (Freeman & Herron, 2004, p. 376). This differential of forces is closely tied to the distribution of reproductive control. Generally, males have a virtually unlimited supply of extremely small and inexpensive gametes, meaning they are rarely the bottleneck in the reproductive process (Alcock, 2005, p. 373; Freeman & Herron, 2004, pp. 376-377). Conversely, females produce large, relatively expensive gametes in far lower quantities, a trend that usually dictates their role as the limiting reproductive reagent (Alcock, 2005, p. 373; Freeman & Herron, 2004, pp. 376-377). In addition, females often provide the greatest proportion of parental care to their offspring, with their reproductive success depending mostly on how many eggs they can produce and how well they can raise their young to maturity (Alcock, 2005, p. 373). Though the situation is reversed in some species, males resort to polygyny, obtaining as many mates as possible in order to enhance their reproductive success (Freeman & Herron, 2004, p. 376). With a higher variation in mating success, males are most frequently exposed to greater forces of sexual selection than females (Freeman & Herron, 2004, p. 377).

Through this difference in selection forces, which results in dimorphism, sexual reproduction leads to heterogamy (i.e., different sized gametes) and the co-evolution of the sexes (Kokko, Jennions & Brooks, 2006). In particular, extreme cases of dimorphism, as in

the seemingly prohibitively costly ornaments of the peacock's tail, should be evolutionarily impossible due to natural selection. Nonetheless, Darwin proposed that sexual selection could lead to the evolution of such characters because "...although some mate-acquiring attributes surely shorten a male's life directly or indirectly, they may increase his lifetime reproductive success by enabling [him] to secure mates in competition with others" (Alcock, 2005, p. 374).

To obtain a greater command of the concepts of natural and sexual selection, the means by which they can act on individuals and populations must be fully comprehended. Direct selection acts upon individuals that have behavioural and physical characters that allow them to pass their genetic information on to direct descendents whereas indirect selection (i.e., kin selection) works upon individuals that have characters that enhance the reproductive success of their close relatives, effectively passing on their own genes (Alcock, 2005, pp. 452-453). Furthermore, sexual selection can act upon a species in two main ways: Intrasexually, as males compete with males and females compete with females (e.g., sperm competition, infanticide and combat) and intersexually, as males and females attempt to attract members of the opposite sex (Freeman & Herron, 2004, p. 380; Moller & Pomiankowski, 1993). Though male-male intrasexual selection is a considerable force in many species, it is female preference for certain desirable males that makes the final decision since females controls the sought after eggs (Alcock, 2005, p. 365). Currently, the scientific community speaks more of the similarities than the differences between intersexual and intrasexual forces of selection as they are both vital to the process of evolutionary change, both conferring some individuals in a population with greater reproductive success (Alcock, 2005, p. 330).

The peacock's elaborate tail can hardly be considered an advantage in intrasexual selection as it makes for a poor weapon in combat and confers no benefit to the peacock's ability to copulate successfully (Johnstone, 1995; Petrie & Halliday, 1994). For this reason, and because of the relative control that females have over reproduction, peahen preference is considered the driving force of sexual selection acting on peacocks (Petrie & Williams, 1993; Ryan, 1993). Since peacocks neither provide food for peahens during courtship nor contribute post-mating parental care, hypotheses that focus on the transfer of direct benefits to the peahen and the advantage of 'good parenting' are inadequate in explaining the evolution of the male's tail (Alcock, 2005, p. 351; Petrie, 1994; Petrie & Williams, 1993). Complicating the interaction further is the odd behaviour of male lekking, which cannot be considered in terms of direct selection, but is best explained by theories of kin selection (Petrie, Cotgreave & Pike, 2009; Petrie, Krupa & Burke, 1999).

From this understanding of the multiple forces at play in the secondary sexual characters and reproductive behaviours of *P. cristatus*, each must be addressed in as much isolation as is possible in order to establish their contributory evolutionary roles. At the same time, each force, and its evolutionary effects, must be regarded in the context of a highly integrated system of interactions, which may not be entirely possible to disentangle. Initially, to be able to discuss female preference and kin selection as forces of evolution, a more thorough knowledge of *P. cristatus* must be obtained.

### ***Pavo cristatus*: Boastful Lekkers**

The aptly named Indian peacock, also known as the common or blue peacock, originates from the Indian subcontinent (Gadagkar, 2003). Sexual dimorphism in this species is highly pronounced with the male being both larger on average and more ornately decorated. Peacocks weigh between four and six kilograms, their bodies measuring more than a metre long with another metre of tail made of about 250 long feathers, 150 of which have a decorative coppery-coloured eye-spot with a purplish black centre (Gadagkar, 2003). They have several additional ornaments that they use as tools of sexual communication such as “...an iridescent blue ventral color; an iridescent green dorsal color; an exaggerated crest; bare, white facial skin patches; and long spurs” (Moller & Petrie, 2002). In contrast to the fan-crested peacock, brilliantly clad in blue and green, the peahen is only three to four kilograms in weight, is less than a metre long and is clothed in brown, dull feathers, bearing a crest but no elaborate tail (Gadagkar, 2003).

Peacocks, as in other species that have great inequalities in mating success across their male population, neither go out in search of mates nor defend a group of females or resources, but rather form polygynous leks where they fight to control a small display area (i.e., mini-territory or lekking ground) (Alcock, 2005, p. 398; Freeman & Herron, 2004, p. 195; Gadagkar, 2003; Petrie, Krupa & Burke, 1999). There are several theories as to why males of different species form leks, including the ‘hotspot’ hypothesis where males are thought to congregate on commonly used female travel routes; ‘hotshot’ hypothesis, which proposes that subordinate males gather around attractive males to have a chance at mating; and simple female preference hypothesis (Alcock, 2005, p. 398). The latter hypothesis focuses on the benefit males obtain from lekking due to the increased number of females that arrive per male, as a result of their clustering (Petrie, Krupa & Burke, 1999). Though direct sexual selection is widely considered to be closely correlated with the evolution of secondary sexual characters, across many bird species this correlation is only intermediate in its ability to maintain them over evolutionary time, indicating that the indirect selection of female preference is paramount (Gontard-Danek & Moller, 1999).

To answer the question of the role of female preference in the elaboration of the peacock’s tail, whether or not ornamentation even has an influence on mating success must be ascertained. Petrie and Halliday (1994) hypothesized that if ornamentation does have an effect then the number and arrangement of eye-spots on the tail should be variables that determine mating success among males of the species. They performed breeding experiments in order to test this hypothesis by first modifying the tails of a test group of peacocks, removing some of their eye-spots between mating seasons. The peacocks with eye-spots removed performed markedly worse in reproductive efforts than in the previous year compared to the control group that was left unaltered. From this experiment they concluded that, at least in part, the peacock’s tail has evolved due to female preference.

Next, specifically what peacocks do in order to attract the peahens’ attention must be determined. In a lek, the males display their ornate tails by raising them in the air, fanning them out and then performing an elaborate dance, drooping their half-spread wings to the ground, strutting, prancing and shivering (Gadagkar, 2003). Though this

behaviour appears ungainly and detrimental to survival, it provides clues as to the advantage that greater elaboration of the tail confers (Freeman & Herron, 2004, p. 599; Gadagkar, 2003). Indeed, this same advantage has been observed in 40 other species of birds, spiders, insects and fish in which greater reproductive success is achieved by males with larger bodies, more frequent courtship displays and more ornaments or weapons (Gadagkar, 2003). Clearly, female preference for these attributes in peacocks must contribute more of a reproductive advantage to males than their costs detract from their ability to survive (Johnstone, 1995). Based on the observable preference that peahens have for peacocks with greater numbers of eye-spots on their tails, sensory stimulation during courtship undoubtedly has an influence on reproductive success (Alcock, 2005, pp. 353, 355).

It is the fact that peacocks display themselves in leks that emphasizes the point that they themselves do not have an evolutionary mechanism to monopolize access to females in order to increase their own reproductive success (Freeman & Herron, 2004, p. 388). This is a realization that has allowed the theory of female preference to become the most widely accepted explanation (Freeman & Herron, 2004, p. 388). Still, the question remains as to what it is about these showy males that gives females that choose them a reproductive advantage (Johnstone, 1995; Ryan & Rand, 1993). There are four current models of sexual selection to explain the evolution and maintenance of the peacock's tail: the sensory bias, chase-away, Fisher's (i.e., runaway) and good-genes (i.e., the handicap principle) hypotheses (Wiens, 2001). The influence that each of these evolutionary explanations has had on the evolution of the peacock's tail is not fully understood (Alcock, 2005, p. 351; Johnstone, 1995). Simply knowing that female preference drives sexual selection in this case does not differentiate between these various hypotheses because each is internally valid while external validation is very difficult to test (Rand, 1993; Ryan & Rand, 1993). These hypotheses must be understood separately before the most explanatory mechanism can be elucidated.

#### **Four Theories of Female Mate Preference**

First, the hypothesis of sensory bias indicates female preference is the result of a visual, auditory or olfactory based predilection for certain male characters (Wiens, 2001; Ryan & Rand, 1993). This preference is for attributes that provide a direct advantage to survivability and reproduction are the side-effects of neurological constructs that are used, or were used at some other time in evolutionary history, to confer adaptability (Freeman & Herron, 2004, p. 398; Johnstone, 1995). Avoidance of predators and heightened foraging ability are two examples of previously evolved mechanisms that can be exploited by an elaborate character (Wiens, 2001). Over evolutionary time, it is female preference that evolves first, with the male character evolving to take advantage of it (Freeman & Herron, 2004, p. 398; Ryan & Rand, 1993).

Second, the chase-away selection hypothesis proposes a combination of sensory bias as the origin of a character with the subsequent loss of the female preference for it (Wiens, 2001). In this hypothesis, the extreme characters found in the male evolve as a

result of a conflict between the sexes, as the males are continually selected for greater and greater exploitation of the females' sensory bias while the females are likewise selected for their ability to resist the males' exploitation (Alcock, 2005, p. 351). This competition 'chases' the female preference away, but leaves the male character intact (Alcock, 2005, p. 351; Wiens, 2001).

Third, Fisher's run-away selection hypothesis is used to explain how selection can lead to an elaborate male character through the entirely random association of female preference with a male character (Alcock, 2005, p. 351; Johnstone, 1995; Ryan & Rand, 1993). Population genetics models are used to explain how, through linkage disequilibrium with genes for preferences, genes for displays can evolve through evolutionary hitchhiking (Johnstone, 1995; Ryan & Rand, 1993). As a result of this correlation between what is only a mild preference for a non-extreme male characteristic to begin with, selection drives them to extremes over time (Gadagkar, 2003; Wiens, 2001; Ryan & Rand, 1993). This line of thinking has led to the 'sexy sons' hypothesis in which females that choose showy males bear sons that have those characters and daughters that are likely to prefer them (Andersson & Simmons, 2006; Alcock, 2005, p. 357). This can be understood as a self-reinforcing mechanism of the co-evolution of the female preference and the male character (Freeman & Herron, 2004, p. 377). The co-evolution of these characters allows them to become exaggerated, being compounded by new mutations and 'running away' to such extremes that the only reason for the persistence of the male character is the female preference that maintains it (Alcock, 2005, p. 357; Gadagkar, 2003).

Fourth, the good-genes hypothesis is the most popular explanation, focussing on the utility of female preference in detecting genetic quality in potential mates and the necessity of male response in evolving costly signals to display their underlying quality (Ryan & Rand, 1993). Similar to run-away selection, the character and the female preference for it co-evolve, but dissimilarly, the females are thought to choose males because of their showy handicap rather than in spite of it (Gadagkar, 2003; Ryan & Rand, 1993). In run-away selection, peahens are proposed to choose peacocks because they are beautiful, even though they are not the best at surviving, which allows sexual selection to outweigh natural selection, but under the good-genes hypothesis the male's showy tail is an honest signal (i.e., reliable indicator) of better survivability, even though at first glance it would seem to be of detriment (Gadagkar, 2003; Wiens, 2001).

In order to resist false representation of good genetic quality, a signal, such as the peacock's tail, must have a cost (i.e., handicap) to survival, which makes it difficult for individuals without good genetics to present the showy character; this handicap prevents individuals with poor genetics from cheating the system, a concept known as Zahavi's handicap principle (Gadagkar, 2003; Penn & Potts, 1998; Johnstone, 1995). The stability of an honest signal depends on the breadth of the divide between the expense of the signal to individuals with low genetic quality, which are sending it deceptively, and to individuals of high quality that are displaying it honestly (Owens, 1995). The greater the expense, the greater the stability of the signal will be (Owens, 1995). The handicap, therefore, provides no benefit to the male, but is the honest advertisement of mate value to the female onlooker, which is selected for and passed on to the next generation (Alcock, 2005, pp. 351,

356). Though not readily accepted as a valid explanation when it was first proposed, Zahavi's handicap principle has drastically changed the way that evolutionary biologists understand animal communication and behaviour (Gadagkar, 2003). More convincing evidence of its superior ability to explain the peacock's situation must still be evaluated (Gadagkar, 2003).

Since reproduction is a costly investment, for females especially, the decisions that individuals must make in order to maximize mating success are particularly important (Petrie & Williams, 1993). Iteroparous species like *P. cristatus* benefit most when they invest more in reproductive efforts with greater potential benefits (Petrie & Williams, 1993). Greater investment in reproductive efforts with highly ornamented peacocks should, therefore, correlate with a direct or indirect benefit to peahens (Petrie & Williams, 1993).

Petrie and Williams (1993) conducted controlled breeding experiments in pens, which verified that peahens do in fact invest more heavily in reproductive efforts with peacocks that have more elaborate tails. Having ruled out the influence of larger peacocks being able to fertilize more eggs, they tested three means by which peahens can increase their investment in reproduction: Investing earlier, producing more eggs and making larger eggs. From these experiments, it was found that tail elaboration (i.e., number of eye-spots) and length are positively correlated with greater peahen investment in number of eggs while affecting neither timing of egg-laying nor egg size significantly. In fact, peahens that mated with the peacocks with the largest tails had nearly twice as many eggs as those that mated with males that had the smallest tails. These researchers further noted that similar trends of greater reproductive effort correlated with more elaborate males have been recorded in studies of zebra finches (*Poephila guttata*), southern green stinkbugs (*Nazara viridula*) and monogamous swallows (*Hirundo rustica*). As in these other studies, the data on peahen reproductive investment indicate that the selective pressure exerted by female preference strongly favours these exaggerated secondary sexual characters, pointing toward either run-away selection or the handicap principle as a primary mechanism, but not differentiating between them (Petrie & Williams, 1993).

Not discounting the other three theories, for they all have some respective ability to explain the evolution of the peacock's tail, the handicap principle seems to provide the greatest resolution in analyzing this issue (Gadagkar, 2003). To be convinced of this hypothesis over Fisher's run-away hypothesis though, the question of whether or not males with showy tails survive better must be answered. More succinctly, it must be seen as to whether or not showy tails are an honest signal. The simple answer to this question, and confirmation that the peacock's tail is an honest signal, comes from observational studies that clearly demonstrate that peacock's with more elaborate tails survive better than less ornate peacocks when under predation by foxes (Alcock, 2005, p. 359). This evidence supports the hypothesis that female preference selects for good-genes in males. To further evidence this hypothesis, what the peacock's tail is signalling must be fully appreciated. This will explain the mechanism by which the peacock's handicap drives the maintenance of such an astounding character.

## The Peacock's Handicap: An Honest Signal

The peacock's handicap appears to be an honest signal, but what is it signalling? The means by which males communicate sexual signals must be addressed for an answer to this question. For a male's signal to be communicated there must be variation in the population (Ryan & Rand, 1993). Across various taxonomic groups, this variation manifests as a difference in courtship display (e.g., birds), release of a pheromone (e.g., mammals and insects), discharge of electricity (e.g., fish) and mating song (e.g., birds, frogs and insects) (Ryan & Rand, 1993). The male's signal differentiates itself from the background noise that tends to mask it by evolving towards an extreme version of the character (Ryan & Rand, 1993).

Though in most animal species the expression a secondary sexual character is testosterone-dependent, many male characters in birds are derived differently (Owens, 1995). In *P. cristatus* spurs and wattles are testosterone-dependent, yet castrating a peacock has no effect on its plumage (Owens, 1995). On the other hand, removing a peahen's ovaries causes it to develop male plumage, indicating that the male's showy characters are the neutral state of development (Owens, 1995). Different than testosterone-dependent expression, condition-dependent expression of secondary sexual characters depends on the fulfillment of physiological demand for resources, which only strong, healthy peacocks can achieve (Moller & Petrie, 2002). Only individuals that are both generally healthy and that are genetically resistant to debilitating parasites are capable of overcoming this physiological barrier and expressing such characters (Moller & Petrie, 2002). Researchers have found that immune function is a particularly strong indicator of condition-dependence because strong immune response is only possible for individuals that are in prime physical condition (Moller & Petrie, 2002).

As described in listing the species' specific physical characters, the peacock has more than one way of communicating its fitness, and there are three hypotheses to explain this multi-level signalling: The various components of these signals indicate different aspects of the individual's combined suitability; the different components are redundant signals of part of the same aspect of fitness; or some of the signals being given are unreliable indicators of the individual's condition, but since they are not very costly, they persist nonetheless (Moller & Petrie, 2002). In that some features of the peacock's sexual ornamentation are positively condition-dependent on some aspects of immunocompetence and others are not, the third explanation seems to fit the best (Moller & Petrie, 2002). Each peacock does as well as it can in producing elaborate signals for peahens, but some are not as good as others because of the condition-dependence of these characters, which provides females with an honest signal (Gadagkar, 2003).

Other research has shown that there are physiological differences between peacocks with varying lengths of tails. For example, those with longer, more ornate tails have greater fat reserves as a percent of their body weight (Gadagkar, 2003). This condition-dependent expression of the peacock's secondary sexual characters draws the connection between the health of each individual and what sort of mate attracting

characters it can display (Gadagkar, 2003). Also, condition-dependent expression data such as these are direct evidence that the peacock's tail is an honest indicator of good genetics (Gadagkar, 2003).

To support this evidence for condition-dependent expression, the relative ability of different peacocks to fend off parasites has been investigated (Gadagkar, 2003). Moller and Petrie (2002) studied the condition-dependent expression of the peacock's tail in relation to immunocompetence, as measured by cell-mediated immunity and humoral immunity. They found that tail length is condition-dependent on cell-mediated immunity, but not dependent on humoral immunity. Also, they found that number and size of eye-spots is not condition-dependent on either measure of immunocompetence. Earlier research having focused on a range of parasites that had little to no effect on the overall fitness of their hosts, this study provides stronger support for the good-genes hypothesis because it places emphasis on the peacock's anti-parasite defences. These evidences have established that, in peacocks, secondary sexual characters are "...honest indicator[s] of a male's resistance to parasites", allowing peahens to acquire better genes for their young (Penn & Potts, 1998). In different species though, the reason why females choose males with these honest signals is to avoid contracting parasites or diseases during mating and to obtain greater parental investment from the father (Penn & Potts, 1998).

Despite this weighty evidence for the handicap principle as a primary mechanism, for complete differentiation between the various hypotheses, multiple levels of analysis are required. Though behavioural characters such as female preference, male-male competition and predation risk do not leave fossils, phylogenetic studies can be used to understand the progressive appearance and disappearance of male secondary sexual characters. From the recent expansion of knowledge in the realm of bird phylogeny, surprising trends have been discovered (Wiens, 2001).

In resolving phylogenetic trees, the most parsimonious explanation is most often sought since the evolution of characters is more frequent than the loss of characters. In contrast, it has become apparent that the loss of elaborate male characters in bird clades outnumber gains five to one (Wiens, 2001). The validity of these findings has been confirmed through isolating these character losses in deeply nested clades that usually show the character, but that uncommonly contain changes (Wiens, 2001). In such cases, it is more parsimonious for the character to have been lost once than to have evolved multiple times, but in order for a character to be lost, forces must be present that overcome the forces of sexual selection that reinforce it (Wiens, 2001). Understanding how these male characters and female preferences are lost in some bird groups will have weighty influence on the emerging consensus on models to explain sexual selection in *P. cristatus* (Wiens, 2001). Greater resolution in these models is required to continue the effort to integrate phylogenetic, experimental and theoretical studies of *P. cristatus* evolution (Wiens, 2001).

Significant support for the handicap principle as the primary explanation for female preference has been presented in this analysis. Also, this model for explaining the evolution of the peacock's extraordinary tail leads into a discussion on its interesting lekking behaviour.



## Why Ugly Birds Lek

Peahen preference determines which peacocks will have relative success in mating, therefore, how is variation among peacocks maintained, and why do ugly peacocks with unimpressive tails bother to lek with their more well-endowed companions (Andersson & Simmons, 2006)? Since peacocks do not provide parental care, their lekking behaviour exposes peahens to little risk, allowing the direct benefits of sperm competition and sperm selection to spread in populations (Lank *et al.*, 1995). Peahens obtain access to the best genetics (through accurately evaluating peacocks' honest signals), and so benefit from mating with the most attractive peacock in a lek.

Whereas an increased number of mates is a reproductive advantage that polygynous peacocks exploit, larger leks attract more peahens, allowing attractive peacocks to access more mates through displaying of their secondary sexual characters (Gadagkar, 2003; Johnstone, 1995). Yet, the reason for unattractive peacocks to lek with attractive competitors is less clear since they place themselves in direct comparison against others that have an advantage over them (Petrie, Krupa & Burke, 1999). Rather than trying their chances at finding a willing female elsewhere, unattractive peacocks add to the reproductive success of attractive competitors through boosting the numbers of their lek. Are unattractive peacocks being altruistic in their lekking behaviour (Gadagkar, 2003)?

Peacock lekking behaviour can largely be described by the model of kin selection in which close genetic relatives group together in order to pass their genes on indirectly to the next generation (Gadagkar, 2003). "Birds of a feather lek together..." because their presence increases the affectivity of their relatives' reproductive effort, helping them to pass on their genes, which, or course, are also their own (Gadagkar, 2003). For this mechanism to function, peacocks must be able differentiate their brothers from non-relatives (Gadagkar, 2003). To demonstrate this, Petrie, Krupa and Burke (1999) designed experiments based on the kin selection hypothesis that all peacocks that participate in a lek consisting of related individuals receive an indirect fitness benefit even if they do not mate. They used DNA fingerprinting of groups of peacocks to demonstrate that closely related individuals do in fact lek together. To back up these findings they released groups of related and unrelated peacocks that had had no prior contact, allowing them to set up *de novo* lekking grounds. When they found that related birds set up lekking grounds near to each other, they concluded that peacocks display a form of kin association without even knowing their relatives or using environmental cues as guides. Therefore, social learning is not a prerequisite for kin selection, which means that indirect selection has a greater influence on peacock social (specifically, mating) behaviour than previously understood (Petrie, Krupa & Burke, 1999).

Peacocks are able to learn who their relatives are so that they can indirectly pass on their genes by participating in a large, peahen-alluring lek with their best looking brothers. Furthermore, to estimate the heritability of male ornaments and other morphological characters in peacocks, Petrie, Cotgreave and Pike (2009) conducted breeding experiments. Their findings revealed a high level of heritability in characters under selection by female

preference (e.g., tail length) and insignificant heritability for characters that had little to do with fitness (e.g., tarsus length, body weight and spur length). This evidence builds on earlier studies that showed that highly heritable characters are maintained in *P. cristatus* even when they are subjected to great directional selection.

## Conclusions

The handicap principle is gaining support as a favoured model for describing female preference, which drives the evolution of complex secondary sexual characters such as the peacock's elaborate tail. The degree of tail ornamentation that a peacock displays is its primary means of sexual communication, as an honest signal of its immunocompetence and general genetic quality. Peahens that mate with peacocks with larger tails exert more effort in reproduction because they receive better genes for their offspring. Continued work must be conducted to resolve phylogenetic trees for the gain and loss of extraordinary secondary sexual characters in birds in order to unify the evidence behind the handicap principle though. Also, there must be more research to explain in greater detail the interaction between condition-dependent characters and the anti-parasite immune response in a wide range of animal species.

Lekking behaviour is well explained by the kin selection hypothesis, which points to the indirect benefit that 'ugly' peacocks obtain from promoting the reproductive success of their attractive brothers. Siblings have social recognition mechanisms for finding each other and setting up lekking grounds together. This understanding increases the body of knowledge behind social learning in birds, but there is continued work to be done in explaining population dynamic models for the persistence of genetic variation among peacocks. Work in this area will integrate with research being done to explain the 'lek paradox', presently area of interest among sexual selection theorists.

Together, these two avenues of sexual selection research continue to provide support to Darwin's original theory of sexual selection that is used to explain what the theory of natural selection seems incapable of describing. In conjunction with similar research in various species of fish, insects, birds and spiders, Darwin's questions will continue to be laid to rest, and new doorways in evolutionary biology will be opened. As greater understanding of the evolution of physical oddities and strange animal behaviour is obtained, the possibilities for research into the quandaries of human evolution (e.g., altruism and odd sexual behaviour) will become a more pronounced reality.

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**Biology 416**  
**Research Paper Topics**  
**2009**

Although I have suggested some topics below, you are free to choose any topic in evolutionary biology that interests you. Ideally your paper should synthesize fossil evidence, molecular data, and ecological evidence (as much as is possible or relevant). As well as books, you are expected to use primary literature, evaluate some of this literature, and contrast and evaluate the arguments or hypotheses presented.

UNDER NO CIRCUMSTANCES WILL I ACCEPT PAPERS ON DISK!!

**Your paper must also explore a theoretical position rather than just being a paper on comparative biology.** For example, if you wished to write about the evolution of the kidney (H.W. Smith wrote a famous book on this called *From Fish to Philosopher*), you might explore arguments about whether different parts of the body can evolve at different rates and the proposed mechanisms for differential evolution. As an illustration, amphibians differ quite widely in body form, but the kidney has stayed basically the same.

**Length:** 3000 - 4000 words.

**Some suggestions:**

- Evolution of a taxonomic group (e.g., frogs, confers, disease organism, etc.) or the evolution of some specialized aspect of a group (e.g., evolution of developmental patterns in frogs or host specificity in disease organisms)
- Has the “Out of Africa” (one final migration) hypothesis swept the field too soon? Do other arguments offer useful critiques or modifications of the single origin model?
- Dramatic morphological changes (e.g., the fin-to-limb transition in vertebrates) involve many small modifications over millions of years (fossil vs molecular evidence).
- Does environmental change open up new adaptive zones and promote speciation? What is the nature of fossil and contemporary evidence? (This could be usefully linked to global warming.)
  
- Models of adaptive radiation. Which are supported by fossil and molecular evidence?
- In what circumstances have organismal/morphological evolution and molecular evolution (e.g., cryptic variation) been shown to operate independently of each other?
- Major transitions in molecular evolution (e.g., transition from prokaryotes to eukaryotes, evolution of deuterostomy vs. protostomy, etc.)
- The role of sexual selection in evolution (e.g., in a specific taxon)
- The evolution of molecular mechanisms underlying physiological and phenotypic responses to different environmental conditions (e.g., response to heat shock in invertebrates or the evolution of different flowering times as angiosperms extend their range)
- The role of development in the evolution of a taxon (e.g., sticklebacks)
- Molecular population genetics and biogeography (focus on a specific group)
- The evolutionary history of a group of molecules (e.g., hemoglobin)
- The evolutionary history of a developmental gene family (e.g., Pax 6)
- The evolutionary possibilities of endangered species and remnant populations

- Does evolutionary medicine offer a useful perspective for dealing with human disease?
- The evolution of morphological diversity is directly related to the evolution of genetic regulatory pathways

**Your research paper proposal is due on January 28<sup>th</sup>** (although you should talk to me about your general ideas before you invest time in investigating resources for your topic). Your proposal should contain a description of your topic, the theoretical aspects you intend to investigate, the type of evidence you intend to consider (fossil evidence, molecular data, and/or ecological evidence), and cite at least 5 resources (references) you have found and a list of what are looking for.

**Reference check is due the week of February 13<sup>th</sup>.** I expect to examine at least 10 papers.

**• You will not be able to submit a final paper unless you complete these requirements.**

**The final paper is due on March 20<sup>th</sup>.** I encourage you to give me an early draft of your paper for feedback.

### **Assessment Criteria for Papers**

**A papers. Work of exceptional quality.**

The content, organization and style are all at a high level and move the discussion well beyond what is presented in classes or in textbooks. The written work demonstrates excellent comprehension of the subject and is written in a clear, scholarly fashion. The organization is logical and develops a strong thesis or argument step by step without irrelevant material. The paper successfully integrates theory and empirical evidence, uses existing research and literature (print and electronic media) and offers a critical or original perspective on the literature as part of the paper's arguments. Some of the research papers used have been critically evaluated. The paper finishes with a strong conclusion based on sound scientific reasoning, use of appropriate theory, critical thinking, and original interpretations or ideas.

**B papers. Work of good quality with no major weaknesses.**

All of the required elements of the project have been fulfilled. The writing is clear and explicit and clearly presents a thesis or argument. The paper is generally well written. The coverage and demonstrated comprehension of the topic is more than adequate although there may be minor problems in organization of the paper. There is good use of existing knowledge (original and summarized) on the subject but this material may be presented with inadequate interpretation. Some of the research papers used may have been critically evaluated. A reasonable degree of scientific reasoning, critical thinking, and original thought is shown. The paper presents a sound conclusion that uses appropriate theory and there is evidence of original interpretations or ideas.

**C papers. Adequate work.**

All or most of the required elements have been included, although some inadequacies of conception or coverage are evident. A fair comprehension of the subject is demonstrated, but some weaknesses in content, style, organization, and critical awareness are evident. There are errors in grammar, punctuation, and spelling. Use of literature may be apparent but mostly relies heavily on textbooks or summaries rather than original works. While understanding of the topic is adequate, there is little originality. The conclusion is short and non-theoretical.

**P papers. Acceptable work.**

Some of the required elements are missing. Inadequacies of conception and coverage are evident. Although parts of the topic appear to be understood, overall comprehension of the topic has not

been well demonstrated. There may be unresolved contradictions in the material presented and there is little demonstration of critical awareness. Weaknesses in content, style, organization, grammar and punctuation are common. Limited literature sources, usually textbooks or summaries, are used without interpretation. A satisfactory conclusion is usually lacking.

**NC. Unsatisfactory work.**

Many of the required elements are missing. The paper is unacceptable in both coverage and comprehension of topic, and in presentation.

**Unacceptable papers.**

Papers which display clear evidence of cheating will be given a zero grade. In general, cheating includes plagiarism from published or electronic sources (failing to acknowledge the use of someone else's language, information or ideas), copying another student's work, and falsifying or manufacturing data.

## **Biology 416 Guidelines for Writing a Research Paper**

**Keys to a successful paper:**

The Introduction engages the reader's interest in the topic. Show the reader what makes your topic both significant and problematic (i.e., full of interesting issues). Set out the thesis (i.e., main message) or research question that you are going to investigate in your paper. Tell the reader how work in this area contributes to evolutionary theory. Give the reader an overview of your paper, either by providing a brief summary of the arguments or forecasting the body of the paper.

The body of the paper reveals your response to the questions and issues raised in the introduction. You make this as persuasive as possible through appropriate analysis and argumentation (including effective use of evidence), and through the analysis and critique of how the evidence contributes to existing evolutionary theory.

In the conclusion you may need to summarize your arguments and relate them back to the theory described in the introduction (if you haven't done so already). You should explain the significance of your findings and perhaps outline the areas in which conclusions cannot yet be reached.

**Audience and role of the writer:**

Write to another member of the class who knows less than you do about the topic and is interested but skeptical about your findings.

Your role is to synthesize the best of current thinking on the topic.

**Grading criteria:**

1. Quality of the narrative (the reader gets a clear picture of the thesis you are trying to convey) 10 points
2. Quality of causal analysis (clearly stated points, good support that is related to the thesis or question, plausible and convincing arguments based on data, adequate quantity of recent papers, high quality of sources) 60 points
3. readability (clear organization as described above, good use of headings, clear sentences with no confusing passages) 20 points
4. Grammar and correctness 10 points

