Is the peacock merely beautiful or also honest?*

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Darwin proposed the theory of sexual selection to account for the evolution of extravagant secondary sexual characters often seen in males because he argued that utilitarian natural selection cannot permit their evolution. Although the idea of sexual selection was disbelieved or neglected for a long time, today it constitutes an active area of research. Starting with Darwin, the enormous, cumbersome train of the peacock has been the prime example of sexually selected traits. And yet, almost nothing relevant to sexual selection was known about the peacock until very recently. In the last ten years or so, observations and experiments on a free-ranging, feral population of the Indian peacock in the Whipsnade Park in Bedfordshire in the UK and some experiments in a commercial peacock farm that breeds birds for food and as show birds, by Marion Petrie and her colleagues have finally justified the peacock as an icon of sexual selection by female choice. The peacock appears to fulfil nearly every expectation of the theory of sexual selection: peahens prefer peacocks with elaborate trains probably recognizing them by the symmetry of their trains and benefit from doing so because of improved survival of their chicks. Peacocks with elaborate trains themselves appear to be better survivors with larger fat reserves and higher levels of immunocompetence. These findings support theories which suggest that peacocks with elaborate trains are selected because of the handicap they carry rather than in spite of it. Thus the peacock's train is not merely beautiful but is also an honest indicator of male quality. Although the peacock is deeply entrenched in Indian mythology, culture and folklore and it is widely distributed in the country, research from India has regrettably made no significant contribution to recent research justifying the peacock as a prime example of sexual selection and making it a frontrunner in modern studies of sexual selection.

Natural selection and sexual selection

We all know how easy it is to fall in love with our pet ideas and theories even if they are fairly trivial. It is remarkable therefore that Charles Darwin maintained, even as he wrote his *Origin of Species*[1], that natural selection is inadequate to explain some features of the natural world. What Darwin had in mind were the conspicuous, extravagant, often cumbersome and almost wasteful, secondary sexual characters seen in males of many animal species—the antlers of many deer, the colours, calls and displays of many male insects and birds and above all, the train of the peacock. In *The Descent of Man and Selection in Relation to Sex*[2], Darwin argued that such characters could not have been shaped by natural selection as they were likely to be detrimental to the survival of their bearers, being wasteful in terms of resources and energy and making them more vulnerable to predators. To account for such characters, Darwin proposed the theory of Sexual Selection that he said operates because of 'the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction'. In other words, what an individual loses in terms of lower probability of survival may be more than compensated by increased probability of getting more and better mates.

Male–male competition and female choice

Darwin proposed two mechanisms of sexual selection—male–male competition and female choice. The antlers of deer and the horns of antelopes and indeed of many beetles, help males to compete with other males of the same species for access to the best or largest number of females. Such male–male competition was easily accepted by Darwin's contemporaries. But clearly the peacock's train could hardly be helpful in male–male battles. If peahens prefer to mate with peacocks with most elaborate trains for some reason however, then the situation would be quite different. Darwin therefore argued that characters such as the peacock's train must be selected due to female choice. Any reduction in the probability of survival of a peacock, on account of his enormous train which makes his getaway from a predator clumsy, can be more than compensated by better access to females. But why should peahens prefer peacocks that can barely escape from predators? Darwin argued that females have a sense of beauty and are excited and charmed by the extravagant ornaments and displays of the best males. Darwin's contemporaries refused to accept this idea and found it impossible to believe that deer and birds, let alone insects, could have a sense of beauty. Thomas Henry Huxley, Darwin's self-appointed advocate of the

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theory of evolution, who was sometimes referred to as Darwin's bulldog, tried to persuade Darwin to drop the idea of sexual selection altogether. Among Darwin's contemporaries, Alfred Russell Wallace, the co-discoverer of the principle of natural selection, being 'more Darwinian than Darwin himself', came out most strongly against the theory of sexual selection, arguing that natural selection was adequate to explain everything in nature, including the peacock's train[3]. See Hiraiwa-Hasegawa[4] for an interesting commentary on why the world was so slow in accepting Darwin's theory of sexual selection.

Fisher's run-away selection

If Darwin's contemporaries were sceptical of his theory of sexual selection, his successors ignored it almost completely, for nearly a hundred years. Today, however, sexual selection is one of the most vigorously pursued branches of modern evolutionary biology. Both male–male competition as well as female choice are widely accepted mechanisms of sexual selection. Much progress has been made in thinking about, and to some extent in understanding, why females might choose particular males—what's in it for them if the males are not necessarily the best survivors? Ronald Fisher, one of the architects of the genetical theory of evolution was the first to propose a model of female choice. Fisher argued that at first, the slightly exaggerated male character, such as an intermediate sized train of the peacock might well be correlated with male quality (ability to survive). At this stage females will be selected to prefer peacocks with long trains. Later the very fact that peahens prefer males with elaborate and long trains can drive selection on peacocks to grow trains even longer and more elaborate than is good for their survival. Fisher called this process run-away selection[5]. It is ironical that Fisher, who produced precise mathematical models for all his theories, left this one alone unformulated in mathematical language and therefore untested even for its plausibility. But today there exist mathematical models that justify Fisher's arguments—run-away sexual selection can indeed work in the manner that Fisher thought it might. A crucial aspect of Fisher's theory, and one that contrasts with other theories (see below), is that peahens continue to be selected to prefer peacocks with long trains even after such peacocks are no longer the best survivors. They are supposed to do so because they find peacocks with long trains beautiful and are compensated for mating with less than the best survivors because their sons will also have long trains and will be preferred by peahens of the next generation. Will this process of ever increasing length of the trains ever stop? Yes, it will but Fisher's prediction was that it will not stop just when peacocks with the longest trains are the best survivors but well after the trains have become much longer than is good for their survival. We may therefore think of Fisher's theory as one which predicts that the peacock's long train is preferred by the peahen merely because it is beautiful and not because it is also an honest signal of the peacock's ability to survive.

Zahavi's handicap principle

Of the many theories proposed for sexual selection in general and female choice in particular, the one most different from Fishers' run-away selection theory is the handicap principle proposed by Amotz Zahavi. Zahavi made the radical suggestion that the peacock's long tail is selected precisely because it is a handicap, not in spite of being a handicap. By carrying around such a handicap of a tail and by not yet having succumbed to a predator, the peacock reliably demonstrates to females that he is indeed very fit[6]. Zahavi derived from this idea a far-reaching general principle that animal signals in general must impose a differential cost, a handicap, on the signaler in order to be reliable and thus resistant to faking[7]. It is the disproportionate cost to low quality males that is imposed by the handicap which prevents them from cheating. The scientific community rejected Zahavi's ideas outright. Several distinguished theoretical evolutionary biologists wrote mathematically sophisticated papers arguing that the handicap principle cannot work. One paper was actually entitled 'The handicap mechanism of sexual selection does not work'[8].

Then everything changed in 1990 when Alan Grafen published two papers showing, with the aid of more economically inspired mathematical models, that Zahavi's handicap principle can indeed work, both in the evolution of honest signals in general and in the context of sexual selection[9,10]. Today, Zahavi's handicap idea and the more general, costly, honest signal idea are widely accepted and have considerably altered the way in which we model and study animal communication and behavioural evolution. The well-known evolutionary biologist John Maynard Smith has graciously admitted publicly that he was wrong in hastily concluding that Zahavi's idea was in error. But of course Maynard Smith said it in his inimitable style[11]: 'I was cynical about the idea when I first heard it, essentially because it was expressed in words rather than in a mathematical model. This may seem an odd reason, but I remain convinced that formal models are better than verbal ones, because they force the theorist to say precisely what he means. However, in this case my cynicism was unjustified. It has proved possible to formulate mathematical models showing that what Zahavi called the "handicap principle" can lead to the evolution of honest signals.' In contrast to Fisher's run-away selection theory, we may think of Zahavi's theory as one which predicts that the peacock's elaborate train is preferred by the peahen not merely because it is beautiful but because it is also an honest signal of the peacock's ability to survive.

What do we know about the peacock?

From Darwin's time to the present, the peacock has been the most enduring icon of sexual selection. The train of the peacock represents an extreme example of conspicuous, extravagant, cumbersome and wasteful secondary sexual characters that could hardly have evolved by utilitarian natural selection. But how much do we really know about the peacock and where indeed did Darwin get his information about the peacock? Starting with the Pharaohs of Egypt, the peacock has been introduced to many parts of the world. But it turns out that we knew almost nothing (of relevance to sexual selection) about the peacock until very recently. As for Darwin, he had to rely entirely on anecdotal information from game keepers and others. For instance, he writes that 'Dr Jerdon insists that the beautiful plumage of the male (Peacock) serves to fascinate and attract the female' and that 'Mr Bartlett, at the Zoological Gardens, expressed himself to me in the strongest terms to the same effect. It must be a grand sight in India "to come suddenly on twenty or thirty pea-fowl, the males displaying their gorgeous trains, and strutting about in all the pomp of pride before the gratified females".' And the rest was his own conjecture. For example, he wrote, 'Nor can we doubt that the long train of the peacock . . . must render them more easy prey to any prowling tiger-cat than would otherwise be the case.' As we shall see below, modern studies of the peacock, that justify its status as an icon of sexual selection, have only begun in the 1990s.

Variously described as the common peacock, blue peacock or Indian peacock, *Pavo cristatus* is native to the Indian subcontinent. Even less is known about the green or Javanese peacock (*Pavo muticus*) or the more recently discovered Congo peacock (*Afropavo congensis*) (which incidentally does not have a train) so that everything that we will discuss below pertains to the Indian peacock. The peacock has a very special place in Indian mythology and culture—a vehicle of the god Karthikeya or Subrahmanya, the enemy of venomous serpents, a symbol of grace and charm, a love messenger, recipient of a boon from the god Indra in the form of a thousand eyes on its feathers, an essential item in temple paintings . . . the list goes on[12]. Not surprisingly, the peacock was India's choice when The International Council for the Preservations of Birds passed a resolution that every nation designate one species as its national bird[13]. The familiar male peacock is a large pheasant weighing 4–6 kg and measuring over a metre from head to end of tail and over 2 m to end of its full train (Figures 1–6). It has a fan-shaped crest of wire-like feathers on top of the head, brilliant glistening blue neck and breast and a spectacular long train decorated with some 250 long feathers, about 150 of which are decorated with a purplish black-centred coppery eye-spot. The female is remarkably different, weighing only 3–4 kg, measuring less than a metre, mostly brown in colour and relatively dull and drab, with a crest but not the train[14–18]. The peacock is a lekking bird[19]. A lek is a mating arena where an aggregation of males display together and compete for mating with females visiting the lek. Typically only one or a small number of the males get to mate with most of the visiting females so that why so many additional males should spend their time and energy at a spot where they get few or no returns, remains a paradox. In peacock leks, males display by means of

Figure 1. A peacock displaying his ornamented train (This and all the following photos were taken by the author in the peacock island in Berlin-Wansee, Germany. The Indian peacock was introduced into this 1.5 km long and 0.5 km wide picturesque island in 1797.)

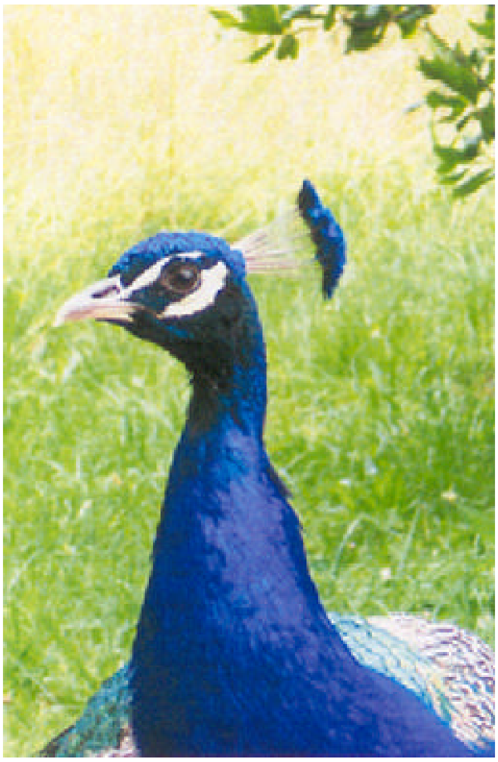

Figure 2. The crest of the peacock.

an elaborate dance. The peacocks erect and fan out their trains, drooping their half-open wings to the sides and strut and prance from one foot to the other, shivering from time to time to produce a spectacular shimmering, psychedelic display. When the train is not erect (or cannot be erected as for example, after a night's rain), it is literally dragged along on the ground. Almost all modern information about the peacock, especially as it relates to the theory of sexual selection, comes from recent studies of free-ranging peacocks by Marion Petrie and her colleagues, in Whipsnade Park in Bedfordshire in the UK, a 541-acre park administered by the Zoological Society of London since 1931.

Figure 3. A peacock with train folded and held in the way it is normally dragged along as the bird walks.

Figure 4. A peahen (note the marked sexual dimorphism between the peacock and peahen).

Do peahens prefer peacocks with elaborate trains?

Recall that Darwin suggested male–male competition and female choice as two possible mechanisms of sexual selection. Thus, if the peacock's train has evolved as a result of sexual selection then the train must either be helpful in male–male combat or it must be that peahens prefer to mate with peacocks with elaborate trains. It seems unlikely that the train can possibly help in male–male combat. In Darwin's words, 'The peacock with his long train appears more like a dandy than a warrior . . .'. Perhaps peahens do prefer peacocks with elaborate trains as Darwin suggested. It is remarkable that almost no one had attempted to find out if this is true until the 1990s.

Starting from October 1987, Marion Petrie and some of her colleagues began observing a population of free-ranging, feral peacocks in Whipsnade Park. Not surprisingly, one of the first questions they asked was about the sexual preferences of peahens. Following a lek consisting of 10 peacocks, Petrie and her colleagues observed 33 copulations, of which a single male was responsible for 12 copulations while some males got none. More pertinently, there was a clear correlation between the number of eye-spots a male had on the feathers in his train and the number of peahens that he was able to mate with (Figure 7). It must be mentioned that several other factors potentially affecting male mating success were examined but only the number of eye-spots proved significant[20]. This is not surprising because it is the eye-spots that really appear, at least to us, to give the dancing and shivering peacock

Figure 5. A dancing peacock (front view).

Figure 6. A dancing peacock (back view).

its psychedelic character. Matt Ridley has gone to the extent of suggesting that the train is merely a vehicle for carrying the eyes and that female choice is achieved by the perfect array of eyes in the expanded fan-like train that has a hypnotic effect on the peahen[21]. Of course there was a lot of variation among males both in the number of eye-spots and in the number of peahens they managed to mate with. Over 50% of the variation in mating success could be attributed to variation in the numbers of eye-spots. Surely there are other factors that affect a male's mating success but the number of eye-spots in his train is an important determinant of mating success. A more recent study by Shahla Yasmin and Yahya from the Aligarh Muslim University in India has confirmed that peacocks are very variable in their mating success and that some measures of their tail length and call complexity are also correlated with mating success[22].

Suggestive as they are, such correlational studies cannot give decisive answers because correlation does not necessarily imply cause and effect. The number of eye-spots may be significantly correlated with mating success but that does not really prove that high number of eye-spots causes high mating success. Both the numbers of eye-spots and mating success may be correlated with an unknown, third factor. For instance, physically strong males may have more eye-spots and may also be preferred by peahens but peahens may prefer them because they are physically stronger and not because they have more eye-spots; peahens may detect physical strength by some other means. For this reason our conclusions from correlational studies can only be suggestive but not definitive. Cause and effect are better inferred from experimental studies. For example, if one can artificially increase or decrease the number of eye-spots on a peacock, then his mating success must increase or decrease as expected. Such evidence would be more powerful because we leave physical strength or any other possible third factor unaffected in the experiment. This is the approach that Marion Petrie and Tim Halliday took in another study. It is not easy to increase the number of eye-spots but it is fairly easy to decrease their number. Petrie and Halliday caught 22 full-trained peacocks, cut away 20 eye-spots from 11 of them (the experimental group) and handled the remaining 11 in the same way but did not remove their eye-spots (the control group) and released all of them. They then compared the mating success of these males, relative to their mating success in the previous year before the manipulation. There was a sharp decline in the mating success of the experimental males (with 20 eye-spots removed) compared to the previous season. No such decline was observed in the case of the control males (those caught and released without reducing the number of eye-spots)[23] (Figure 8). This gives much greater confidence in the conclusion that peacocks with higher numbers of eye-spots have greater mating success.

Whether peahens actively choose males with elaborate trains (with a large number of eye-spots) or whether males with elaborate trains compete with other males in some other way needs to be examined. To do this, Petrie and her colleagues made more detailed observations on the behaviour of the females. In the 33 copulations they managed to observe, never did it happen that a peahen mated with the first peacock that courted her. On average peahens visited three different males before making up their mind. On 11 occasions Petrie and her colleagues observed the complete sequence of events from the time of arrival of a female until she copulated with a male. In 10 of these sequences, the male that was finally chosen had the highest number of eye-spots of all the males sampled by the peahen. It was thus clear that who mates with whom was not decided by the males but indeed by the females who exercised an active choice in the matter. An especially fascinating finding was that some females mated repeatedly with the most preferred males, conse-

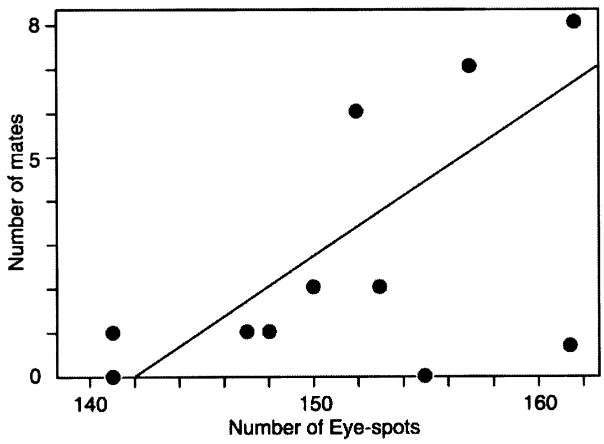

Figure 7. Relationship between male mating success and the number of eye-spots in the male's train. Redrawn from Petrie *et al.*[20], with permission, © 1991 Elsevier.

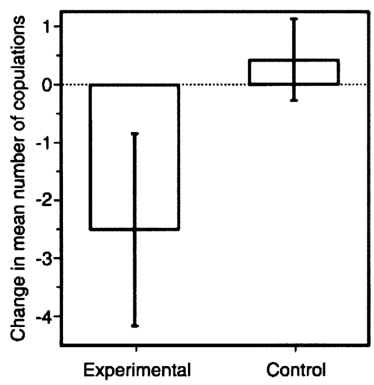

Figure 8. Change in the number of copulations between seasons for those males who had 20 eye-spots removed (experimental; six males) in comparison with those males whose trains were not manipulated (control; 15 males). Redrawn from Petrie and Halliday[23] (Permission requested).

quently preventing those males from mating with other females[24]. All these findings vindicate Darwin's conjecture, albeit some 120 years later, that the peacock's train could have evolved at least partly due to sexual selection by female choice.

How do peahens recognize the best males?

We saw above that peahens prefer to mate with peacocks possessing the most elaborate trains, trains with the largest numbers of eye-spots. But how might peahens recognize such peacocks and reliably distinguish them from other less endowed peacocks? The most successful peacocks have over 150 eye-spots and removing even 20 of them had a significant effect on their mating success. It therefore seems unlikely that peahens would actually count the number of eye-spots that different peacocks carry on their trains. In recent years it is being realized that fluctuating asymmetry is a sensitive parameter that often correlates with the inherent quality of animals and their ability to cope with environmental stress. Fluctuating asymmetry is a term coined in 1932 by the German biologist Wilhelm Ludwig to refer to random departures from bilateral asymmetry. Rather precisely controlled genetic programs are required to produce animals with perfect symmetry. Symmetry is therefore one of the first causalities when an animal is less than very fit and indeed when even the fittest animals face environmental stress during development[25–27]. It may be that symmetry of the peacock's train is easier for peahens to assess rather than to count the number of eye-spots. If the fittest males have the highest number of eye-spots in their trains they may also well be the most symmetric individuals. Manning and Hartley of the University of Liverpool in the UK decided to test this idea[28]. The number of eye-spots on the left and right sides of the peacock's train will not always be exactly the same but the question is how asymmetrical can the trains be? Manning and Hartley[28] therefore measured the degree of fluctuating asymmetry as the number of eye-spots on the side with the greater number of eye-spots minus the number of eye-spots on the side with the lesser number of eye-spots. That number ranged from zero in some individuals (the perfectly symmetric ones) to as much as 17 in others (the most asymmetric ones). Manning and Hartley found a strong positive correlation between the number of eye-spots on peacocks' trains and the degree of fluctuating asymmetry (Figure 9). This means that peacocks with the highest numbers of eye-spots tended to be most symmetric.

We still cannot conclude that peahens use fluctuating asymmetry as a cue for male quality because no one has selectively removed eye-spots from one side of the train to create asymmetric peacocks and examined if there is a decline in their mating success. Another possibility is that females simply assess the length of the train but again, no one has yet altered the length of the train and measured mating success. Train length, number of eye-spots and fluctuating asymmetry are all inter-correlated features of peacock trains and we do not still know which one or which combination is used by peahens when they choose their mates. The answer to this question must be within experimental reach. However if the psychedelic, hypnotic effect of the shimmering, rattling train during his dance is what excites a peahen, as Matt Ridley has suggested, it will need a really ingenious experiment indeed.

Why do peahens prefer to mate with peacocks having the most elaborate trains?

There remains a major unsolved problem in sexual selection theory, especially when it is thought to depend on female choice. What do the females gain from mating with males having the most elaborate, ornamented secondary sexual characters? This is especially problematic in lekking species because in such species the males provide no territory, no parental care for the chicks, nothing more than sperm. This has come to be known as the lek paradox[29]. In our context, what advantage do peahens who mate with peacocks with the most elaborate trains get? Is it possible that they get excellent sperm, meaning sperm carrying excellent genes that help make particularly healthy and viable chicks? If the much sought-after father provides no help with parental care, he better provide at least good genes. In a carefully controlled experiment, Marion Petrie tested this idea[30]. She isolated eight free-ranging full-trained displaying lek males into separate pens and gave each of them four randomly chosen naive adult peahens. The resulting eggs were removed and artificially incubated under identical conditions so that any systematic differences between the offspring of the different males could be attributed to the father's genetic makeup. Measuring the weight of all the chicks on day 84 of their lives and measuring their survival after two

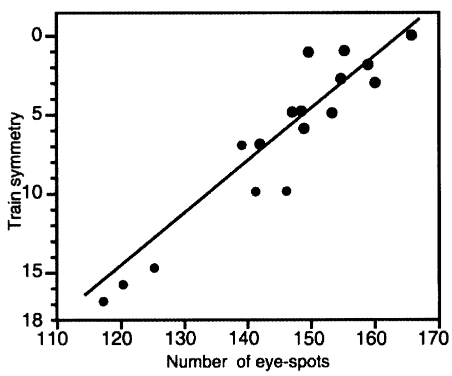

Figure 9. The relationship between train symmetry and the number of eye-spots per train. Redrawn from Manning and Hartley[28], with permission, © 1991 Elsevier.

years, she found significant differences between fathers in the weights and probability of survival of their offspring. Indeed she found that males with larger eye-spots in their trains (size of the eye-spots is easier to measure from the shed feathers as compared to counting the total number of eye-spots in each male) tended to have larger offspring on day 84 and survived better at the end of two years (Figure 10). This is part of the recently accumulating evidence that when certain kinds of males are preferred even though they provide no territory or parental care, the females gain good viability genes from these males. Having lagged embarrassingly behind in studies of sexual selection, the peacock is now among the front-runners in solving the mysteries posed by the sexual behaviour of animals.

Are beautiful peacocks really fitter?

Recall an important distinction between the predictions of Fisherian run-away selection and Zahavi's handicap principle with reference to the survival abilities of males with elaborate secondary sexual characters. Fisher predicted that the train of the peacock has grown beyond what is good for its survival and it is maintained merely because females continue to prefer males with elaborate trains while Zahavi argued that peacocks with elaborate trains survive better despite the handicap of the elaborate train. Not surprisingly, Marion Petrie was interested in the survival ability of peacocks with different kinds of trains. Such data are hard to come by except through serendipity. It seems strange to say so but she got lucky! Five peacocks under her observation and for whom she had data on mating success were killed by foxes in Whipsnade Park. For comparison Petrie included data on all the 43 peacocks she had observed (she excluded one that was killed by a car!) in an analysis that attempted to ask if peacocks with elaborate trains survive poorly as predicted by the Fisherian run-away selection theory or survive

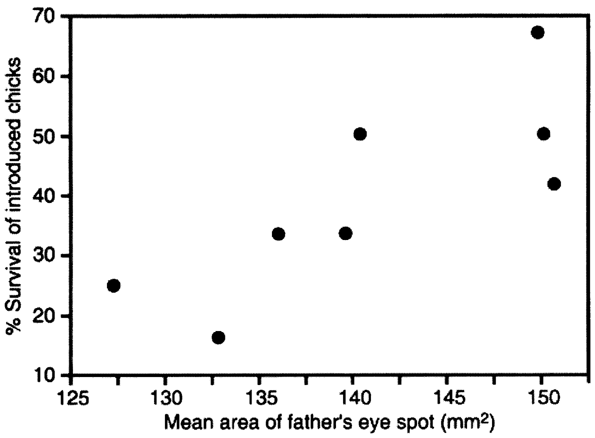

Figure 10. The relationship between the proportion of offspring surviving and the size of the eye-spots in their father's train. Redrawn from Petrie[30], with permission, © 1994 Nature Publishing Group.

better as predicted by Zahavi[31]. Of these 33 peacocks, 22 had copulated at least once each while 11 had not copulated even once in the previous season. Although there were twice as many males successful at copulation, only one of the five predated birds fell into this category of having been successful at copulation while the remaining four predated peacocks had remained completely unsuccessful. This suggests that peacocks chosen by peahens are likely to survive predation better than males rejected by the peahens. Petrie also found that the predated peacocks had somewhat fewer numbers of eye-spots than surviving peacocks and had significantly shorter trains than surviving peacocks. Few though these data are, they do not support the idea that peacocks with long and elaborate trains are poor survivors. If anything they suggest that peacocks with long and elaborate trains are better survivors than their less beautiful neighbours. A similar conclusion is now being reached for many other species. Conducting a meta-analysis of 122 examples of sexually selected traits from 69 studies of 40 species of birds, spiders, insects and fish, Jennions and his colleagues have found that males with larger ornaments or weapons, greater body size or higher rates of courtship generally show better survival and longevity[32].

Why don't all peacocks grow long and elaborate trains?

If peahens prefer to mate with peacocks sporting the most elaborate trains why do not all peacocks grow such trains? If an elaborate train is an honest signal of a good quality male then it follows that all peacocks should not be capable of growing equally elaborate trains and hence peahens can use the peacock's train as a reliable cue of male quality. Some evidence supporting this claim is now beginning to accumulate. Marion Petrie and her colleagues culled 17 peacocks (it is remarkable how few peacocks have been sacrificed for all her research) and did so as part of an operation to reduce the number of peafowl in the park. They used this unique opportunity of having access to research material (which those of us who work with flies and bees so easily take for granted), to ask about other ways in which peacocks with elaborate trains may be different from those with less elaborate trains. Their results showed that peacocks with longer and heavier trains and those with a larger proportion of feathers with eye-spots, had larger fat reserves per unit body weight[33]. This has come to be known as condition-dependent expression of secondary sexual characters because only males in the best condition of health can sport the most elaborate secondary sexual characters. Condition dependent train elaboration in peacocks thus provides further evidence that the elaborate trains of peacocks reflect their superior genetic quality. In their search for the sources of honesty of ornamented males, evolutionary biologists have begun to study not merely the general condition of their health as reflected by fat reserves for example, but also at their ability to mount an immune response against parasite infection. In collaboration with Anders Pape Møller of the CNRS in Paris, Marion Petrie has initiated such research with the peacock too[34]. The first results reveal a complex picture. Some features of the peacocks such as train length are positively associated with immunocompetence while others such as size of the eye-spots are negatively associated. Although more work needs to be done in this field, it appears that not all peacocks can sport the most elaborate trains and each peacock probably does the best it can, providing peahens an honest measure of male quality.

Why do the not-so-beautiful peacocks hang around the lek?

The lek mating system presents many mysteries. The one we addressed above concerned the advantage for females of going through the trouble of choosing the most elaborately ornamented male if all that the male offered her was sperm. Our answer was that the most ornamented males also provide sperm with the best genes that give a substantial advantage to his chicks in their growth and survival. Another mystery of the lek is that if the best males corner all the matings, why should the lesser males bother to hang around the lek? Why should they choose to display and attempt to find mates at a site where they face a stiff competition from better males? The successful peacocks probably benefit from the presence of the unsuccessful ones because a larger group of peacocks must serve to attract peahens to a lek. Success here is not a matter of chance either, because peahens prefer peacocks with the most elaborate trains. Are the unsuccessful peacocks then behaving altruistically and merely helping the successful ones?

Many other cases of apparent altruism, such as the case of sterile workers in social insect colonies working to help their queens to reproduce, have been successfully explained by inclusive fitness theory[35]. According to this idea proposed by Hamilton in 1964, altruism directed towards close genetic relatives can be favoured by natural selection, or a form of natural selection that has come to be known as kin selection. Thus sterile workers in most social insect colonies and helpers in some species of cooperatively breeding birds and mammals are close genetic relatives of the breeding individuals they help. Because close genetic relatives share genes in common, helping a close relative is also a way of increasing the representation of one's genes in the population. If the numbers of copies of an altruist's genes added to the gene pool due to his or her helping a relative is more than the number of such copies lost due to the altruist's failure to produce offspring, then such altruism can actually be a superior evolutionary strategy compared to selfish reproduction. Kin selection theory predicts therefore that if the peacocks with not-so-elaborate trains are selected to spend their time and energy at leks where they get few or no matings, and their presence merely helps peacocks with the most elaborate trains to attract and mate with more and better peahens, then peacocks with less elaborate trains must be closely related to the peacocks with more elaborate trains whom they seem to help. Recent developments in DNA-based technology provide increasingly powerful and sophisticated methods to determine genetic relatedness between individuals. Using one such method called multilocus DNA fingerprinting (which simply means comparing DNA sequences simultaneously in several genes), Marion Petrie and another set of colleagues discovered that peacocks display close to their kin[36], prompting Paul Sherman to coin the limerick 'Birds of a feather lek together'[37]. To positively confirm that kin selection indeed favours peacocks with not-so-elaborate trains who join leks, even if they do not get to mate with peahens, will require more detailed measurements of the costs (to the unsuccessful peacocks) and benefits (to the successful peacocks) of lekking behaviour. Nevertheless, these preliminary data suggest kin selection as a possible force that might promote the formation of leks.

Another interesting, if paradoxical, finding to emerge from this study is that peacocks recognize their brothers and lek preferentially with them even if they have hatched from eggs that had been removed after laying and mixed up with eggs of non-relatives. This suggests that peacocks have some way of discriminating their brothers from non-relatives even if they have not grown up with and learnt the characteristics of their brothers. Such kin recognition without the involvement of social learning is another topic being actively researched today[38].

So, is the peacock merely beautiful or also honest?

In the beginning of this article, we saw that although the peacock has always been an icon of sexual selection, almost nothing of relevance to sexual selection theory was known about the peacock until recently. In just about the last ten years, the situation has changed dramatically. Almost entirely on account of the work of Marion Petrie and her colleagues, nearly every expectation about the peacock, arising from its status as a prime example of sexual selection as driven by female choice, has been put to test. Indeed the peacock today is a front-runner in studies of sexual selection, mate choice and the handicap principle. In the beginning of this article, we also contrasted Fisherian run-away selection and Zahavian handicap principle as a contrast between peahens choosing peacocks with elaborate trains either because they simply find them beautiful (even if they are not the best survivors) or because they perceive in them an honest signal of quality (they are good survivors, in spite of being handicapped by their enormous and expensive trains). Clearly much more work needs to be done especially in clarifying the relative roles of train length, number of eye-spots, size of eye-spots, proportion of feathers with eye-spots, etc., in defining 'elaborateness' of the peacock's train. Nevertheless, everything we have learnt during the past ten years supports the idea that the elaborate and ornate train of a peacock is an honest signal of his health, vigour, survival ability and good genes. Thus, the peacock is also honest and not merely beautiful. Having answered the question raised in the title, this would be a reasonable way to end this article but I cannot bring myself to do so without lamenting on the fact that almost none of this work was done in India. After all the peacock is our national bird and we proudly recall its prominent status in Indian mythology and folklore. It is widely distributed in India and in some places it has almost attained the status of a pest. More damning than all of this is the fact that all the work done on the peacock could easily have been done by any Indian scientist with little or no money, equipment or laboratory facilities. What was needed and what was obviously lacking however was the combination of an interest in natural history and an understanding of the theoretical foundations of modern evolutionary biology. That's something to think about . . . for our students, teachers, researchers and managers of science and education.

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