1 A Darwinian Selection Based Explanation of Peacock's Tail

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4

5 Abstract

6 There is no satisfactory explanation for why peacock possesses a tail, presence and especially
7 courtship display of which makes the organism vulnerable to predation. Here, I present a model
8 according to which in a polygynous mating system a mechanism which increases vulnerability
9 to predation, a Zahavian handicap, evolves when other two mechanisms to identify high-quality
10 males are either absent or are not sufficiently strong. The two mechanisms are: 1) male
11 resource acquisition ability, and 2) male-male competition for females. The three mechanisms
12 are not necessarily mutually exclusive. Assuming the locus for the tail and choosiness to be
13 sex-specific, it is shown through stochastic simulation that sexual selection, mediated by the
14 tail (a Zahavian handicap), leads to higher rate of increase in the quality of the population
15 of tailed peacocks and tailed-choosy peahens (which exclusively mate with tailed peacocks) as
16 compared to the population of tailless peacocks and tailless-choosy peahens (which exclusively
17 mate with tailless peacocks), through a positive feedback, as daughters of tailed-choosy peahens
18 are of higher average quality and, by virtue of not carrying the tail's handicap, also fitness
19 than daughters of tailless-choosy peahens. Also, the fold-change in the population of tailed
20 peacocks and tailless-choosy peahens are higher than the fold-change in the population of
21 tailless peacocks and tailless-choosy peahens, for all combinations of the initial conditions. The
22 same results were got, though in milder form, when tailless-choosy peahens were replaced by
23 indiscriminating peahens (which mate with tailless and tailed peacocks in proportion to their
24 frequencies in the population). Although sons of tailed-choosy peahens have lower average
25 fitness than sons of indiscriminating peahens, this difference is inconsequential, because in a
26 polygynous mating system a single male can potentially mate with every female. The work
27 presented here reconciles Zahavi's handicap principle with Darwin's theories of natural and
28 sexual selection. Further, it is hypothesized that a genotype responsible for producing in males
29 a reliable indicator of high quality (a Zahavian handicap) or paternal care ability generates
30 mating desirability in females towards males possessing the indicator. It is demonstrated
31 through simulation that this cross-gender pleiotropy expedites the evolution of tailed peacocks

32 and tailed-choosy peahens and leads to higher rate of increase in their quality.

33 **Keywords:** Peacock's tail, Zahavi's handicap principle, sexual selection, cross-gender pleiotropy

34 1. Introduction

35 In many species, males possess characteristics such as antlers, ornate tail, and colouration,
 36 and behaviours such as courtship display and song which reduce their fitness and thus cannot
 37 be explained by the theory of natural selection. In order to explain the presence of such
 38 characteristics, Darwin [1] proposed the theory of sexual selection, according to which the
 39 lowered fitness of males possessing such characteristics gets offset by their being more attractive
 40 to females and thus producing more and/or superiour quality progeny than those males which
 41 lack them. But the sexual selection theory did not explain what advantage do progeny of
 42 females which choose males possessing such characteristics have over progeny of those females
 43 which choose other males, so that the evolution of the female choosiness itself could be accounted
 44 for.

45

46 According to Fisher [2], initially the male characteristic and male quality were correlated;
 47 thus, those females which chose males possessing the characteristic left more descendants
 48 than those females which chose males without the characteristic. Thus, in the subsequent
 49 generations, males had evolved heightened form of the characteristic and females had evolved
 50 higher attraction for it. Then a point arrived when further increase in the characteristic's size
 51 had no correlation with male fitness, but still the increase in the characteristic's size and female
 52 attraction for it continued because of the selective pressure created by the latter. In other words,
 53 males possessing the characteristic had more and/or superiour quality progeny simply because
 54 of the female attraction for the characteristic. A few questions can be raised on Fisher's
 55 argument: a) in what way the characteristic was correlated with male quality?, b) how that
 56 correlation came to an end?, and c) what factor compensates for the cost of the extra size of the
 57 characteristic? Additionally, female attraction for a characteristic is not sufficient to cause the

58 evolution and maintenance of the characteristic. This can be seen by considering a hypothetical
 59 example where a fraction of females are attracted to, and thus mates with, males which are blue
 60 coloured, whereas the other fraction of females mates with colourless males. The blue colour
 61 is due to a by-product of defective metabolism. Thus, because of inheriting defective metabolic
 62 genes and getting lower quality parental care, the average fitness of progeny of females which
 63 mate with blue males is lower than the average fitness of progeny of females which mate with
 64 colourless males. This amounts to lower percentage of blue males and females having attraction
 65 for blue males in the subsequent generation. Thus, with each passing generation the percentage
 66 of blue males and females having attraction for them will decrease.

67

68 For a characteristic to undergo positive selection in a polygynous mating system, it should
 69 increase fitness of at least female offspring in terms of them getting good genes and/or better
 70 paternal care. The characteristic may decrease fitness of male offspring to the extent that
 71 only few males survive. The lower survivability of males is inconsequential because in a
 72 polygynous mating system a single male can potentially mate with every female. Natural
 73 selection can be looked at as a feedback mechanism. Genes that increase fitness (“good genes”)
 74 enable the organism to leave more descendants, hence higher presence of the good genes in
 75 the subsequent generation. Genes that decrease fitness (“bad genes”) cause the organism to
 76 leave fewer descendants, hence lower presence of the bad genes in the subsequent generation.
 77 Sexual selection for a characteristic can only escape this loop if the characteristic has no effect
 78 on fitness. Thus, Fisher's argument is tantamount to assuming that the characteristics have no
 79 effect on fitness, which is clearly not true.

80

81 In 1975, Amotz Zahavi [3] proposed the handicap hypothesis to explain the evolution of
 82 the male characteristics and behaviours which, although reduce their fitness, increase their
 83 mating success. According to Zahavi, the presence of such fitness-reducing traits are tests,
 84 as only high-quality males would be able to survive despite incurring a loss in fitness due
 85 to the handicap. Thus, the presence of such traits reliably signals male quality, for males

not possessing such traits may or may not be of high quality. It has been demonstrated that offspring of peacocks with more elaborate train grow and survive better under experimental conditions which are approximately the same as natural conditions [4]. In 1976, Maynard Smith [5] analyzed the handicap hypothesis and concluded that the proposed mechanism does not work, even when the handicap is absent in females. In 1978, Bell [6] carried out a more extensive study of the handicap principle, considering haploid population in monogamous and polygynous mating system. The study found out that the principle can work in a certain condition related to the initial frequency of choosy females. The results of Bell's paper are discussed below. A study by Davis and O'Donald [7] concluded that Zahavi's model cannot work; but because the analysis in the paper is beyond the scope of the present work, results of that work will not be discussed here.

2. Results and Discussion

2.1. Fundamental biological functions

In a naive consideration, life can be thought of as an organism's struggle to leave as many descendants as possible. This, then, demands the organism to succeed in performing at least the following functions: 1) acquire and protect resources, 2) acquire mate, and 3) protect oneself and progeny. For the male gender, the function of mate protection may also be added. In many cases, the female gender has the additional function of gestation to perform. Because resource protection is needed only when resources have been acquired, the function of resource protection may be subsumed into the function of resource acquisition. Further, the functions of protecting progeny and mate (in case mate protection is present) may be subsumed into the need to protect oneself. Arguably, the function of self-protection should also include protecting oneself from parasites and pathogens, because abstractly, parasites and pathogens can be considered equivalent to predators. Also, gestation may be subsumed into resource acquisition. Thus, we are left with three fundamental biological functions, namely resource

112 acquisition, mate acquisition, and self-protection.

113

114 In any mating system, female cannot possess characteristics as indicators of quality that reduce
 115 their fitness, because reproduction primarily depends on them. In a given species, females
 116 which display their quality by a fitness-reducing feature will get outnumbered by females which
 117 don't, because the latter are more likely to survive up to the reproductive age and could invest
 118 advantage due to higher fitness in reproduction (higher quality eggs or better gestation) and
 119 parental care. In monogamous mating system, because each male can mate with only one
 120 female, males also should not indicate their quality by characteristics which reduce fitness.
 121 In polygynous mating system, however, because a high-quality male can mate with several
 122 females, characteristics that reduce fitness can serve as indicator of quality. This is because a
 123 few high-quality males may still survive, and consequently all females can get to mate. Because
 124 the present work seeks to explain the evolution of peacock's tail, the focus will be on how
 125 females determine male quality. Thus, a mechanism, or test, needs to exist by means of which
 126 females can determine male quality. Naturally, fundamental biological functions of males can
 127 serve as the tests. However, because male's resource acquisition ability may also contribute to
 128 his mate acquisition ability, an alternate formulation may be better conceptually. Thus, because
 129 the process of mate acquisition consists of a male displaying his ability to acquire resources
 130 and/or fighting off rival males, it may be better to replace “resource and mate acquisition” with
 131 “resource acquisition and male-male competition”.

132

133 a) Resource acquisition: Males may demonstrate their resource acquisition ability in three
 134 ways. First, by stockpiling resources. Second, by possessing high-investment characteristics,
 135 such as antlers, which are shed and regrown annually. Only those males which are good at
 136 resource acquisition will be able to grow and maintain antlers. Third, by building an architecture,
 137 e.g. nest or bower. Although vast majority of bird species are monogamous, a bird species may
 138 be imagined in which males build multiple nests in order to attract many females. b) Male-male
 139 competition: The male which defeats rival males in a physical confrontation demonstrates

140 his high quality. c) Self-protection: This test is implemented by way of males possessing a
 141 characteristic or displaying a behaviour which increases their vulnerability to predation. The
 142 examples are the peacock's tail plumes, bright colouration of many bird species, and risky
 143 courtship displays and songs. Males which are able to survive in spite of being more vulnerable
 144 to predation are of higher quality than those which are not. It should be noted that the presence
 145 of increased vulnerability to predation post-mating will hamper paternal care in case it is
 146 present. A hypothetical phenomenon can be considered in which males, as part of courtship
 147 ritual, put them in a situation which makes them highly vulnerable to parasitic/pathogenic
 148 infection. Only high-quality males (i.e., having strong immune system) will be able to survive
 149 such ritual. The three functions can also be present in combination. For example, a) antlers
 150 are used as weapons in male-male combat for mate acquisition, and b) male-male fighting
 151 may also be involved in resource acquisition directly or indirectly, that is, in competition for
 152 territorial possession. In the peacock, because the first mechanism is absent and the second
 153 (territorial fight) is weakly present, males are tested on their self-protection ability. Therefore,
 154 a characteristic, the tail, is evolved in males which makes them more vulnerable to predation.
 155 The increased vulnerability to predation exists throughout a peacock's life, but the model only
 156 demands the presence of heightened vulnerability to predation during mate selection process.
 157

Figure 1: Fundamental biological functions for males in a polygynous mating system.

158 **2.2. The evolution of peacock's tail and peahen's choosiness**

159 A haploid population is considered which has i) an autosomal locus for quality, ii) male-specific
 160 locus for tail, and iii) female-specific locus which determines the peahen type. The three loci

161 have two alleles. The first locus has Q (whose values are 1.05, 1.1, 1.2, 1.5, 2) and q (whose
162 value is 1). The second locus has T (tailed peacock) and t (tailless peacock). For the third
163 locus two cases are considered. First in which the two alleles are tailed-choosy, peahens which
164 mate only with tailed peacocks, and tailless-choosy, peahens which mate only with tailless
165 peacocks. Second in which the two alleles are tailed-choosy, peahens which mate only with
166 tailed peacocks, and indiscriminating, peahens which mate with both types of peacocks in
167 proportion to their frequencies in the population. In the present model, an additive model of
168 fitness is employed where fitness is equal to quality minus test (the tail's burden is set equal to
169 q). Because peahens do not have tail, their fitness is equal to their quality, Q. Table 1 shows the
170 equivalence of this model with the additive fitness model of Bell's paper [6]. The simulation
171 was started with initial population of 10^5 male and female offspring each. The initial frequency
172 of the allele Q was taken to be 0.01, 0.05, and 0.1. For simplicity, the initial frequency of
173 tailed peacocks and tailed-choosy peahens were considered to be equal, and were taken to be
174 0.01, 0.05, and 0.1. A tailed peacock having the allele Q reached the reproductive age with the
175 probability $(Q-q)/(Q+q)$, whereas a tailed peacock with the allele q reached the reproductive
176 age with the probability $(q-q)/(Q+q)$; this means that tailed peacocks with the allele q died
177 before being able to reproduce. A tailless peacock or a peahen having the allele Q reached the
178 reproductive age with the probability $Q/(Q+q)$, whereas a tailless peacock or a peahen with the
179 allele q reached the reproductive age with the probability $q/(Q+q)$.

180

181 For a given value of the fitness differential, the initial frequency of the allele Q, and the initial
182 frequency of tailed peacocks, simulation was carried out for the number of generations at which
183 the value of the below-stated quantities stabilized, because of the fixation of the allele Q by
184 natural selection. The quantities are: 1) the ratio of the fold-change in the population of
185 tailed peacocks to the fold-change in the population of tailless peacocks, 2) the ratio of the
186 fold-change in the population of tailed-choosy peahens to the fold-change in the population of
187 tailless-choosy or indiscriminating peahens, 3) the ratio of the fold-change in the quality of
188 the population of tailed peacocks to the fold-change in the quality of the population of tailless

peacocks, and 4) the ratio of the fold-change in the quality of the population of tailed-choosy peahens to the fold-change in the quality of the population of tailless-choosy or indiscriminating peahens. The quality of a population of peafowl is equal to the number of peafowl having the allele Q multiplied by the fitness value of the allele Q plus the number of peafowl having the allele q multiplied by the fitness value of the allele q. In other words, the quality of a peafowl population = (Number of Q peafowls)·Q + (Number of q peafowls)·q.

As argued above, increased vulnerability to predation in peacocks due to the tail enables tailed-choosy peahens to mate with high-quality peacocks, thereby expediting the increase in the quality of the population of tailed peacocks and tailed-choosy peahens. To test this hypothesis, two endogamous populations were considered. The first consisted of tailed peacocks and tailed-choosy peahens, which mate only with tailed peacocks. The second consisted of tailless peacocks and tailless-choosy peahens, which mate only with tailless peacocks. Thus, the second population serves as the control, for natural selection is the only evolutionary force acting upon it. The ratio of the fold-change in the quality of the population of tailed peacocks to the population of tailless peacocks was interpreted as the rate of increase in the quality of peacocks due to sexual selection mediated by the tail. The ratio of the fold-change in the quality of the population of tailed-choosy peahens to the population of tailless-choosy peahens was interpreted as the rate of increase in the quality of peahens due to sexual selection mediated by the tail. The ratio of the fold-change in the population of tailed peacocks to the population of tailless peacocks was interpreted as the rate of the evolution of the tail. The ratio of the fold-change in the population of tailed-choosy peahens to the population of tailless-choosy peahens was interpreted as the rate of the evolution of the female choosiness.

As figure 2 shows, for every combination of the initial conditions all the four fold-change ratios are more than one, demonstrating that the Zahavian handicap leads to higher rate of increase in the quality of peacocks and peahens and expedites the evolution of tailed peacocks and tailed-choosy peahens. The explanation of these results are as follows. The average quality

217 of tailed peacocks which survive to reproduce despite heightened vulnerability to predation is
 218 higher than the average quality of tailless peacocks. Therefore, the average fitness of daughters
 219 of tailed-choosy peahens is higher than the average fitness of daughters of tailless-choosy
 220 peahens. Consequently, more daughters of tailed-choosy peahens survive until the reproductive
 221 age as compared to daughters of tailless-choosy, thereby amounting to higher percentage of
 222 tailed-choosy peahens in the subsequent generation, and so on. In honour of Amotz Zahavi,
 223 I name this positive feedback loop the Zahavian runaway. Alternately, from the perspective
 224 of higher survivability of daughters of tailed-choosy peahens, the mechanism proposed here
 225 may also be called the fitter-daughter principle. Because these daughters will produce tailed
 226 peacocks, the average quality of tailed peacocks also will be higher than the average quality of
 227 tailless peacocks, and the percentage of tailed peacocks will also increase with each generation.
 228 It should be noted, however, that the peacock percentage is not as crucial a factor as the peahen
 229 percentage because the mating system is polygynous, where a single male can potentially mate
 230 with every female. The fixation of the allele Q and consequent stabilization of the fold-change
 231 ratios does not create a conceptual problem, because the struggle between prey and predator
 232 is perpetual. In other words, the prey needs to evolve continuously in order to keep up with
 233 the predator's evolution, and vice-versa. Richard Dawkins reasoned that according to Zahavi's
 234 argument, selection should favour 'the evolution of males with only one leg and only one eye'
 235 [8]. In the light of the work presented here, the reply is that selection could have favoured the
 236 evolution of males with only one leg and only one eye if the genetic mechanism had been such
 237 that the defect was phenotypically restricted to males.

238

239 Notably, all the fold-change ratios decrease as the fitness differential increases. This happens
 240 because with higher fitness differential, effect of natural selection becomes stronger (higher
 241 percentage of tailless peacocks with the allele Q survives), thereby diminishing the role of
 242 the handicap principle, which is mediated through sexual selection. The four fold-change
 243 ratios also decrease as the initial frequency of the allele Q increases. The explanation for
 244 this trend is as follows. The average quality of tailed peacocks is higher than that of tailless

245 peacocks because tailed peacocks having the allele q do not survive to reproduce, whereas
 246 tailless peacocks with the same allele do. With higher initial frequency of the allele Q , fewer
 247 tailless peacocks with the allele q are present, thereby reducing the advantage due to the
 248 handicap. For very low fitness differentials, the population of tailed peacocks and tailed-choosy
 249 peahens went extinct in significant percentages of runs. This was clearly because of very low
 250 survivability of tailed peacocks, and thus low chances of mating between tailed peacocks and
 251 tailed-choosy peahens, when the fitness differential is low. However, once the two populations
 252 sustained up to the sixth generation, they never went extinct.

253

254 The same analysis was carried out by replacing tailless-choosy peahens with indiscriminating
 255 peahens, which mate with tailed and tailless peacocks in proportion to their frequencies in
 256 the population. As previously, for every combination of the initial conditions all the four
 257 fold-change ratios are more than one, though there are a few differences. For all combinations
 258 of the initial conditions, the ratio of the fold-change in the population of tailed-choosy peahens
 259 to the population of indiscriminating peahens is lower than the ratio of the fold-change in
 260 the population of tailed-choosy peahens to the population of tailless-choosy peahens. The
 261 explanation for this is as follows. Because the average quality of tailed peacocks is higher than
 262 the average quality of tailless peacocks, the average quality (and hence also average fitness)
 263 of daughters of indiscriminating peahens is higher than the average quality of daughters of
 264 tailless-choosy peahens. Consequently, more daughters of indiscriminating peahens survive
 265 to reproduce, which lowers the fold-change ratio. Further, as the initial fraction of tailed
 266 peacocks increases, the ratio of the fold-change in the population of tailed-choosy peahens
 267 to the population of tailless-choosy peahens remains constant, but the ratio of the fold-change in
 268 the population of tailed-choosy peahens to the population of indiscriminating peahens decreases.
 269 This is because the likelihood of mating between indiscriminating peahens and tailed peacocks
 270 goes up as the initial fraction of tailed peacocks increases.

271

272 For low fitness differentials, the ratio of the fold-change in the population of tailed peacocks

to the population of tailless peacocks is lower for the case where indiscriminating peahens are present as compared to the case where tailless-choosy peahens are present. For higher values of the fitness differential, the reverse is true. Specifically, in the indiscriminating peahens case, although the number of tailed peacocks is higher, the increase in the number of tailless peacocks is such that the ratio of the fold-change in the population of tailed peacocks to the population of tailless peacocks is lower than the tailless-choosy peahens case, for low fitness differentials. The reason for this result is as follows. Mating between tailed peacocks and indiscriminating peahens has two opposing effects on the growth rate of tailless peacocks: 1) it reduces the growth rate of tailless peacocks by lowering their chances of mating with indiscriminating peahens, and 2) it increases the growth rate of tailless peacocks in the following way. Because the average quality of tailed peacocks is higher than the average quality of tailless peacocks, mating of indiscriminating peahens with tailed peacocks, instead of tailless peacocks, produces higher quality indiscriminating peahens. In the next generation, mating between tailless peacocks and indiscriminating peahens which received the higher quality allele, Q , from their tailed father produces higher quality tailless peacocks. When the fitness differential is high, the former effect dominates because the quality of tailless peacocks increases much more due to natural selection, whose intensity is higher due to large fitness differential, than due to the coupling between tailless peacocks and tailed peacocks via indiscriminating peahens, and vice-versa. The reasoning also explains the result that although the fold-change in the population of indiscriminating peahens increases for all fitness differentials as the initial fraction of tailed peacocks goes up, the fold-change in the population of tailless peacocks, as the initial fraction of tailed peacocks goes up, decreases only when the fitness differential is equal to 2.

295

However, for all fitness differentials, the fold-change in the population of tailed peacocks does not increase as the initial fraction of tailed peacock goes up. This was unexpected because as the initial fraction of tailed peacock increases, more mating events occur between tailed peacocks and indiscriminating peahens. It seems that this discrepancy might be due to very high variance of the fold-change in the population of tailed peacocks at low initial frequency of

301 tailed peacocks. The variance decreased as the initial frequency of tailed peacocks increased.
 302 For the initial frequency of tailed peacocks equal to 0.01, the variance and mean had the same
 303 order of magnitude, whereas for the initial frequency equal to 0.1, the variance was one order
 304 of magnitude less than the mean. The same trend was observed for the fold-change in the
 305 population of tailed peacocks for the tailless-choosy peahens case and also for tailed-choosy
 306 peahens in both cases (i.e., tailless-choosy peahens and indiscriminating peahens cases). In
 307 any case, because the ratio of the fold-change in the population of tailed-choosy peahens to the
 308 population of indiscriminating peahens is more than one, the evolution in this mating scenario
 309 also occurs through Zahavian runaway.
 310

Figure 2: (In the first column, the initial fraction of tailed peacocks and tailed-choosy peahens (f) is equal to 0.01, in the second column $f=0.05$, and in the third $f=0.1$. **(A)** The ratio of the fold-change in the population of tailed peacocks to the population of tailless peacocks. **(B)** The ratio of the fold-change in the population of tailed-choosy peahens to the population of tailless-choosy peahens. **(C)** The ratio of the fold-change in the quality of the population of tailed peacocks to the quality of the population of tailless peacocks. **(D)** The ratio of the fold-change in the quality of the population of tailed-choosy peahens to the quality of the population of tailless-choosy peahens.

311 The study by Bell [6] showed that the handicap principle can work within a certain range of

Figure 3: (In the first column, the initial fraction of tailed peacocks and tailed-choosy peahens (f) is equal to 0.01, in the second column $f=0.05$, and in the third $f=0.1$. **(A)** The ratio of the fold-change in the population of tailed peacocks to the population of tailless peacocks. **(B)** The ratio of the fold-change in the population of tailed-choosy peahens to the population of indiscriminating peahens. **(C)** The ratio of the fold-change in the quality of the population of tailed peacocks to the quality of the population of tailless peacocks. **(D)** The ratio of the fold-change in the quality of the population of tailed-choosy peahens to the quality of the population of indiscriminating peahens.

the initial frequency of choosy females. Specifically, for a given value of the fitness differential (which is equal to $Q-q$ in the present work), there will be a value of the initial frequency of tailed-choosy females, below which the handicap principle cannot not work. However, according to the mechanism proposed here, whatever may the initial frequency of tailed-choosy females be, the handicap principle will always work. That's because the average fitness of daughters of tailed-choosy females will always be greater than the average fitness of daughters of indiscriminating females. This leads to higher percentage of tailed-choosy peahens, and therefore lower percentage of indiscriminating peahens, in the subsequent generation.

Table 1: Equivalence of Bell's additive fitness model [6] and the model in the present work

Allele	Tailed Peacock	Tailless Peacock	Peahen
B	$\alpha + \beta$	$\alpha + \beta + \epsilon$	$\alpha + \beta + \epsilon$
b	α	$\alpha + \epsilon$	$\alpha \epsilon$
Q	$Q - q$	Q	Q
q	$q - q$	q	q

The fitness differential $\beta=Q-q$; the tail's burden $\epsilon=q$; $\alpha=0$

A study [9] showed that peacocks which exhibited frequent behavioural display and had a large number of tail eyespots had better immune system. Peacocks which displayed frequently put themselves at predation risk more often than those which displayed less frequently. Arguably, this behaviour should be heritable. A tail eyespot most probably gives a semblance of a face, and consequently invites more attention from predators. Thus, frequent behavioural display and more tail eyespots translate to stronger test. Only high-quality peacocks are able to pass this test, and daughters of those peahens which mate with such peacocks have higher fitness. Overtime, this will lead to a correlation between high quality (such as better immune system) and frequent behavioural display and more tail eyespots. This result may seem to support the Hamilton-Zuk hypothesis, but an alternative, more general explanation is provided below.

2.3. The Hamilton-Zuk hypothesis

According to the Hamilton-Zuk hypothesis, male secondary sexual characteristics signal resistance to parasites and pathogens [10]. Recently, a comparative genome analysis of Indian peacock [11] reported that the immune system genes of the bird displayed signs of adaptive evolution. The authors observed this result of being supportive of the Hamilton-Zuk hypothesis. However, a more general reasoning can account for the evolution of the immune system genes in peacock [11] and the correlation reported between better immune system and higher frequency of behavioural display and large number of tail eyespots [9], if infection by parasites or pathogens are considered to be a test. A peacock with weak immune system and carrying an infection will sluggishly respond to a predatory attack and consequently will be less likely to survive. This will lead to selection of higher quality immune system. Further, all faculties involved in evading predation, such as the sensory systems and muscles and bones involved in taking wing and flying, will undergo selection for improvement. This may explain the findings of the comparative genome analysis [11] that genes involved in bone morphogenesis and skeletal muscle development showed signs of adaptive evolution.

2.4. Cross-gender pleiotropy

The analysis above is based on the assumption that the locus for the tail is male-specific and the locus which determines peahen type (tailed-choosy, tailless-choosy, and indiscriminating) is female-specific. However, because an ovariectomized peahen develops peacock-type plumage [12], the locus for the tail has to be autosomal. If the tail's locus is assumed to be autosomal, half of the daughters (and also sons) of tailed-choosy peahens will be having the T allele. Therefore with each passing generation the percentage of tailed-choosy peahens having the t allele will get halved. Thus it is not clear why the tail's locus should be autosomal. This led the author to consider a model where all three loci were autosomal and peahens were either tailed-choosy or indiscriminating. Although, due to the lack of computing power, the simulation could not be

done for the number of generations at which the four fold-change ratios stabilize, it could still be observed that the ratios were very low and most likely were not going to become more than one. Mechanistic basis for this result is straightforward: because the initial population of tailed peacocks (and tailless peacocks) had the indiscriminating allele; initially, 50% of the daughters from mating between a tailed peacock and tailed-choosy peahen were indiscriminating.

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As a result, the advantage that tailed-choosy peahens had over indiscriminating peahens in terms of mating exclusively with high-quality peacocks was no more present. 25% of the sons from such a mating will be tailless peacocks having the tailed-choosy allele and another 25% will be tailed peacocks having the tailed-choosy allele. Although half of the daughters from mating between peacocks having the tailed-choosy allele and an indiscriminating peahen will be tailed-choosy, such mating will be very rare to contribute to the evolution of tailed-choosy peahens. The negative results got when the loci for the tail and choosiness are considered to be autosomal leads us to the question: what could be a purpose of the tail's locus being autosomal when normal peahens do not have the tail? I hypothesize that genotype for the tail in peahens contributes, partially or fully, to their desirability to mate with a tailed peacock. Generalizing, a genotype responsible for producing a Zahavian handicap in males generates mating desirability in females towards males possessing the Zahavian handicap. Because, besides good genes, parental care can also increase fitness of the progeny, the hypothesis can be extended. A genotype responsible for producing in males a reliable indicator of high quality (a Zahavian handicap) or paternal care ability generates mating desirability in females towards males possessing the indicator.

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In the earlier simulation, all daughters from a mating between a tailed peacock and an indiscriminating peahen were indiscriminating. By contrast, when genotypes for the tail and female choosiness are assumed to be the same, half of the daughters from mating between a tailed peacock and an indiscriminating peahen are tailed-choosy. Although, half of the sons also are tailless, but that is immaterial in a polygynous mating system. Thus, when genotype for the tail and

female choosiness are identical, the evolution of tailed peacocks and tailed-choosy peahens should be faster. Also, the rate of increase in the quality of tailed peacock and tailed-choosy peahens should be higher. If these predictions are correct, then the four fold-change ratios of the case where genotype for the tail and female choosiness are identical should be higher than the respective four fold-change ratios of the case where one fraction of peahens are tailed-choosy while another fraction is indiscriminating, for all combinations of the initial conditions. Therefore, the ratio of the two ratios should be greater than one. The simulation, however, could not be carried out for the number of generations at which the four fold-change ratios stabilize, because of the lack of computing power. But even for lower number of generations, the prediction turns out to be true, though the result are not presentable.

3. Conclusion

There are at least two reasons why Zahavi's handicap principle found it hard to gain acceptance. Firstly, Zahavi did not state the conditions in which males of a species evolve a handicap, and secondly, he proposed that the evolution of handicaps occur through a non-Darwinian mechanism [13]. Zahavi later suggested that high-quality males may incur lower reduction in fitness than low quality males for the same sized handicap [14]. In simulations done so far, tailed peacocks with the allele Q survived up to the reproductive age with the probability $(Q-q)/(Q+q)$, whereas the survival probability for tailless peacocks was zero (i.e., $(q-q)/(Q+q)$). In other words, the fitness loss was equal for high- and low-quality males. The extreme of Zahavi's suggestion would be to assume that the handicap causes no fitness loss in high-quality males. Thus simulations were done assuming that the handicap in males with the allele Q did not cause a loss in fitness (i.e., the survival probability equal to $Q/(Q+q)$). The results got were the same as those got when the fitness loss was equal for high-quality males and low quality males (data not shown). This was because, as has been mentioned above, in a polygynous mating system only one male needs to survive in order for all females to get the opportunity to

mate. Hence it is shown that a handicap need not cause lower reduction in fitness of high-quality males to make the handicap principle more likely to work.

Additionally, the work presented here also hypothesizes that genotype responsible for producing a handicap in males generates mating desirability in females to mate with males possessing the handicap. This hypothesis has an important implication in the evolution of Zahavian handicaps. Simulations carried out in this work assume the presence of an initial population of peahens which exclusively mate with tailed peacocks, besides the presence of an initial population of tailed peacocks. The need for the simultaneous presence of males possessing a Zahavian handicap and females having mating desirability towards such males makes the evolution of a male handicap and female attraction towards it less likely than if genotype responsible for producing the handicap in males and generating attraction towards it in females is assumed to be identical. In nature, however, genotypes for the two traits need not be identical to produce the evolutionary advantage. Even if genotype in male responsible for producing the handicap generates the mating desirability in females with a moderate probability (say, 0.5), the evolution of the handicap and female attraction towards it will still be faster than when the cross-gender pleiotropy was absent.

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