Theories of sexual selection in animals

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It was more than 100 years ago that Charles Darwin formulated his ideas on sexual selection in The Descent of Man and Selection with regard to Sex (Darwin, 1871). He noticed that animals frequently possessed exaggerated traits which appeared detrimental to their survival, such as the large and decorative train of a peacock and bright plumage colors in many other birds. He recognized that such traits, despite being non-adaptive, may actually be beneficial if they conferred an advantage in terms of increased mating success to their bearers.

In sexually reproducing organisms, each of the offspring has one father and one mother, so the average reproductive success is equal for both males and females. However, if a male gains a disproportionate share of reproduction, he will take away reproductive opportunities from other males, leading to a high reproductive variance among males. On the contrary female will not take away reproductive opportunities from other females, leading to a smaller variance in reproductive success. The higher the reproductive variance, the stronger the effects of sexual selection.

However, theoretical analyses of sexual selection suggest at least three ways sexual selection might come about(1) Female choice: Female mate choice is the subject of a large area of research in behavioural ecology. Over the past three decades, many theoretical and empirical studies have investigated the patterns and consequences of female mating decisions (Andersson, 1994; Shuster and Wade, 2003; Barbosa and Magurran, 2006). If females choose from a variety of males and mate with those who will give those offspring having higher viability or fecundity, then alleles favouring such selection would be favoured and the system should persist.(2) Male-

male sexual competition: if certain males are more able to prevent other males from having access to females, thereby sequestering this desirable resource for themselves, than those dominant males would be selected for and the system of sexual selection would persist.(3) Self-reinforcing choice: if there are alleles that, for whatever reason, predispose females toward males having an extreme character, then those males have an advantage. If that character is heritable, such that her male offspring also tend toward that extreme, then the character may be selected for. Fisher (1950) has termed this “ runaway selection.” Alleles promoting this process may be selected even if they contribute nothing to, or possibly detract from, the viability of the males exhibiting them.

Despite the central role of female preference in sexual selection, and the importance of genetic variation in female preference, female preference is still poorly understood, prompting calls for investigations of the genetic variation in female preference (Heisler, 1984; Bakker and Pomiankowski, 1995; Wagner, 1998; Mead and Arnold, 2004).

Female mate choice has been demonstrated in numerous organisms, including invertebrates and vertebrates like frog, lizards, birds, mammals and has major consequences for the evolution of reproductive strategies (Andersson, 1994; Kokko *et al.,* 2003). The success of males in achieving mating is often linked to the reproductive benefits which females derive (Jennions and Petrie, 1997; Bussiere *et al.,* 2005). Males typically vary in their ability to provide benefits and determining how females detect differences among males in the benefits they offer has revealed much about the processes that drive the evolution of mate choice (Andersson, 1994).

Females use wide varieties of male traits such as larger morphological traits, bigger and brighter color patterns, more vigorous visual displays, and faster, longer, and louder calls to select their mates (Andersson, 1994; Ryan and Keddy-Hector, 1992). Female preferred males with such preferred traits to obtain can provide material resources that increase her or offspring fitness (direct benefits; Heywood, 1989; Price *et al* ., 1993), alleles that increase offspring viability (good genes; Fisher, 1930; Grafen, 1990; Pomiankowski, 1988; Zahavi, 1975), or alleles that affect the attractiveness of male offspring (sexy sons; Fisher, 1930; Kirkpatrick, 1982).

To test whether females directly benefit from mating with preferred male or it is necessary to test the fitness consequences of variation in female mate preference. It is not important whether a study measures the fitness consequences of female preferences or measures the benefits obtained by mating female to account that variation among females is not confounded with variation among males. This is because females with stronger preferences may differ in a variety of ways from females with weaker preferences (Jennions and Petrie, 1997). However the fitness consequences of these differences can be confused with the fitness consequences of female mate preferences. Further, studies in animals have also shown that females which mated with more attractive male could produce more offspring, or invest more in each offspring they produce (Moller and Thorn hill, 1998). This observation suggests that females mating with preferred male obtain direct benefit if they provide nothing to avoid this problem by randomizing the association between trait attractiveness and direct benefit quality (Endler and Basolo, 1998).

If males vary in the direct benefits that they provide to females, or in the costs that they cause females to incur, and if females can directly or indirectly assess the benefits and/or costs of mating with males (i. e., direct benefit quality), then females' preferences based on benefit quality should be favored. Whether preferences actually evolve will depend on a variety of factors, including the costs of being choosy and trade-offs between preferences and other traits.

The most difficult issues confronted in studies of female mate preference are why males should provide benefits to mated female. If male signals correlate with benefit quality, why male signals provides reliable information. To understand this problem by dividing it is potentially useful to direct benefits into three classes as follows. (a) Whether or not females can directly assess benefit quality of male prior to mating and (b) whether or not males use signals to attract females. These can be tested in species in which mating is resource independent because female choice occurs when males offer resources to females in the absence of signaling. (Thorn hill, 1976). If this is true, females can assess the mate for direct benefits prior to mating. In species where mating is a costly phenomenon because they have to face the risk of predation or a risk of parasite transmission, or if females only mate once per reproductive bout. In such situation selection may favor selective mating with those males that offer the highest-quality food items. Thus the female mate preference may favor the evolution of higher-quality direct benefits (e. g., Greater male investment in finding high quality food items). Such direct benefit of female mate preference that makes the evolution of female choice for direct benefits seem simple and straight forward.

Studies have also suggested pathways through which females mated with preferred male may obtain direct benefits. Females may obtain greater direct benefits by mating with the male showing some types of signals, independently of the costs and benefits (Reynolds and Gross, 1992). In animals in which mating is resource is independent in such species. The benefits that male animals provide to females includes nutrients, body parts, and secretions (Gwynne, 1982; Sakaluk, 1984; Thornhill, 1976); access to resources on a territory, including refuges, oviposition or nesting sites, and food (Howard, 1978) more sperm, more viable sperm, or better fertilization ability (Drnevich *et al.,* 2001; Matthews *et al.,* 1997); a variety of products transferred in seminal fluid, including nutritive and defensive compounds (Iyengar and Eisner, 1999; Markow, 1988); male protection, including protection from harassment by other males and from predators (Borgia, 1979) and male care of offspring, including care that frees females to engage in other activities and care that increases offspring fitness (Hill, 1991). Since these male contributions can affect female survivorship reproduction, offspring survivorship and reproduction. For two male contributions may refer to as direct benefits while later two male contribution may referred to as indirect benefits (Grether, 2010). Studies have also pointed out that females may also benefit from mating with certain males not because of the benefits they provide instead these males can impose lower costs on females. For example, females might risk damage from mating with certain male and she preferred to mate with males, which can lower the magnitude of damage (Grether, 2010)

There are growing list of evidence showing that in some taxes males display at fixed courtship, territories known as leks and these males provide only genes (i. e. Sperm) with their mates. (Non resource based mating systems) females receive no resources from males, yet females still show a preference in selecting their mate (Hoglund and Alatalo, 1995). This preference appears to be paradoxical because female of these species only receives genes from the male she selects (Kirkpatrick and Ryan, 1991; Tomkins *et al.,* 2004). Therefore more studies are required to analyze the adaptive significance of age based female mate preference in insects.

The insect whose mating resource independent more appropriate to analyze age based female mate preference for both direct and indirect benefits. Therefore, studies involving accessory glands proteins and sperms are warranted.

Species of the genus *Drosophila* are one such genus whose mating is resource independently, where males does not show parental care or give a nuptial gift to the mated female. They have played an integral role in the development of sexual selection theory, and a great deal is known about the patterns and fitness consequences of female mate choice (Spieth, 1952; Partridge, 1980; Fowler and Partridge, 1989; Chapman *et al.,* 1993; Gromko and Markow, 1993; Hegde and Krishna, 1997; Krishna and Hegde, 2003). Moreover, recent behavioural research revealed that male *Drosophila* varies greatly in its level of interest in females, providing evidence that males have also evolved to selectively mate (Gowaty *et al.,* 2003). Furthermore, the reproductive biology of *Drosophila* is useful for investigating whether the female mate choice is influenced by male quality and the cost of choosing.

Initial studies involving *D. melanogaster* were concentrated on physiological changes associated with changes in parental age, molecular aspects, selection experiments and comparisons of populations that have been generated from individuals of different ages (Parsons, 1962; Wattiaux, 1968; Lints and Hoste, 1974; Ganetzky and Flanagan, 1978; Rose and Charlesworth, 1981; Partridge and Fowler, 1992; Roper *et al.,* 1993; Chippindale *et al.,* 1994; Orr and Sohal, 1994). However, they did not study the parental age effect on the direct benefits of female and offspring fitness.

In order to test good gene model requires the studies involving offspring fitness. However such experiments have been prohibited in many of the animals system. In spite of this very few attempts have been made in laboratory model organism i. e. in *D. melanogaster* (Price and Hansen, 1998). Recently, Prathibha and Krishna (2010) and Somashekar and Krishna (2011) have shown that females of *D. ananassae* and *D. bipectinata* prefer to mate with old aged males more frequently than middle or young aged males. Further, female mating with old aged males obtains both direct and indirect benefits. However, their studies did not involved accessory glands protein and sperm traits. Santhosh and Krishna (2013) involving accessory glands and sperm traits in *D. bipectinata* have shown that female mating with older males obtain a greater quantity of Acps and sperms than females mated with young or middle aged males. Further in *D. melanogaster* Abolhasan *et al.,* (2015) in their study also found that female mate with young males more frequently than middle aged and old males. They also showed that female mated with young male had obtained greater direct benefits (greater quantity of Acps and sperms) than those females mated with either middle

aged or old males. Experimental evidences of these studies in species of *Drosophila* suggest that female mate preference for male age may be an indirect way of assuming the male ejaculate quantity. Therefore more studies of this type in the genus *Drosophila* is very much warranted to frame a hypothesis or generalization with regard to the female preference for male age to understand age based female preference in species of *Drosophila* . Until more species and genera are studied, it will be difficult to draw firm conclusions. Hence, more studies are needed in this regard.

Therefore present study has been undertaken in *D. malerkotliana* . It is a cosmopolitan species and belongs to a member of the *bipectinata* complex of the *ananassae* subgroup (Bock, 1971; Bock and Wheeler, 1972). It has a wide ecogeographical distribution ranging from India through South east Asia and New Guinea to Fiji and Samoa in the Pacific (Bock and Wheeler, 1972). It is a common occurrence in the Indian subcontinent and has attracted the attention of various Indian workers who are using this species for past few years. They have carried out extensive studies on population and behavior genetics of this species and have established the phylogenetic relationship between *D. malerkotliana* and other members of the *bipetinata* complex based on chromosome analysis, hybridization studies and isozyme analysis (Yang *et al.,* 1972; Jha and Rehman, 1972; Hegde and Krishnamurthy, 1979; Singh *et al.,* 1981; Hegde and Krishna, 1997). These findings provide interesting and important information concerning certain aspects of evolutionary genetics of this species. However, in this species it is not known whether females of this species discriminate males on the basis of their age classes, if so what its effect on female direct fitness benefits. Therefore

present investigation has been undertaken in *D. malerkotliana* with the following objective.