Parental investment (PI) and care are features of life history traits. Life history traits are tradeoffs between reproduction and growth, which are two main factors that determine the fitness of an individual (Stearns, 1992). Parental care serves as one of the vital units of the tradeoff between reproduction and growth which directly influences reproductive success (Bonsall & Klug, 2011a; Clutton-Brock, 1991; Klug & Bonsall, 2010; Stearns, 1976). An organism goes through many stages in the life span and at a time succumbs to its age-specific mortality due to various reasons. In such situations, parental care accelerates maturation and increases the survival of infant and juvenile (Clutton-Brock, 1991; Klug & Bonsall, 2010; Kokko & Jennions, 2008; Wilson, 2000). Hence, any parental behavior, which enhances the survival at any stage of life span, is desirable for the survival of infants. If the species show egg mortality then egg care will be favored, and if species show infant mortality then infant care will be favored (Klug & Bonsall, 2010; Kolm & Ahnesjö, 2005; Nussbaum, 1985, 1987; Nussbaum & Schultz, 1989; Shine, 1989). Hence, for parental care to evolve, like any altruistic act, the population should have low dispersal rate that is parents and offspring must be in close proximity. Viviparous animals are excellent examples as the preceding factor of paternal care where young ones are fed until birth. Second, parents should recognize their offspring (evident in almost all societies showing any kind of parental care) (Hamilton, 1964; Lion & Van Baalen, 2007) or at least until the stage where the absence of parental care can result in mortality or might put egg, infant or juvenile at a higher risk. Duration and degree of parental care should be proportionate to the risk and threat at that particular stage. For
instance, in Salamanders and frogs, longer egg stage is selected for care and parental care is restricted only up to the certain stage such as metamorphosis (Nussbaum, 1985, 1987; Nussbaum & Schultz, 1989; Summers, Sea McKeon, & Heying, 2006). Primates, which show almost lifelong care (Fairbanks, 2000), intensity and form of care, differ at each stage of life. An extensive investment is shown at the stage of gestation and lactation during prenatal and period of infancy to ‘umbrella’ care at the juvenile stage that sometimes extends even after juvenile stage (Van Noordwijk, 2012). It is evident in fishes that parental care is directly related to growth rate of offspring and adult development. Species with faster growth of offspring and adult development are linked to lack of parental care because the risk of mortality is less. Whereas species with slower growth rate of offspring and adult development, shows highly developed parental care (for e.g. Winemiller & Rose, 1992). Hence, parental care seems to be better evolved in instances where death rate would have been high (Bonsall & Klug, 2011b; Klug & Bonsall, 2010).

**Basic theory of evolution**

*Variation, competition, and natural selection*

Darwin explained the evolution of morphological and behavioral traits by putting forward certain basic processes. According to Darwin, organisms show differences in their behavior and morphology at two different levels: individual and species level.

He has explained these variations in nature with the help of variation produced under domestication by humans. For instance, development of udder in habitually milked cows and goats as compared to wild populations. In domestic ducks, the wings weigh less than legs, but it is vice–verse in the wild because the ducks in the wild fly more and domestic ducks walk more. These variations are the effect of environmental...
conditions and the use of particular organ, which is a response to the present condition. Many examples can be given of variation under domestication, which provides a framework to understand similar processes in nature. Certain important factors are contributing to the development of certain variations and elimination of certain characters. These features and variations are already present in the individuals while Darwin considers these variations as the result of the effect of conditions of life on the reproductive systems, it is important to note that environmental conditions also determine the extent and direction of development. Environmental conditions such as resource availability, predation, climate, etc. constantly build pressure on an organism to adapt better to the changing conditions and hence induce competition among the individuals of the same species as well as with other species, which has been termed struggle for existence. In the process of adaptation to the changing environmental conditions, certain traits gain an advantage over other traits and hence giving better chances of survival to the organism possessing them. “Industrial melanism” is a fantastic example of how struggle goes on for existence and how certain traits gain an advantage over other traits under changing environmental conditions giving fitness benefit. However, just survival is not enough. The present fitness provides the base for next step of leaving progeny or transferring or replicating one’s genes. It includes the struggle between the members of the same sex to get access to opposite sex, which mostly comprises competition among males for females and female choice. Under domestication, it has been seen often that many peculiarities appeared in one sex get attached to that sex and are often transmitted. Hence, in the process of getting access to opposite sex, where entirely different forces are acting on the two sexes can lead to quite different behavioral tendencies, and morphology, which has been termed as sexual selection. Sexual dimorphism in most species, for example, often-larger body
size of males as compared to females, is the result of sexual selection. Similarly, many of such differences are prevalent in birds and other species.

The individual differences of an organism only serve as the basic unit for differences at the level of species following a large number of generations. Hence, if any variation, even slight, improves the position of an individual, either for survival or for getting access to mates over conspecifics or distinct species under the present environmental conditions will be preserved through the processes of natural selection and harmful alleles will be eliminated. Neutral variations are not carried to the subsequent generation because natural selection works directly on the transmissible characters, which are manifested and affect the individual (Darwin, 1859).

**The paradox of altruism and Hamilton’s rule**

Natural selection explains all traits in terms of the fitness of organism possessing them. Altruism by its very definition reduces the individual fitness. Altruism can be defined as an act that benefits the individual for whom it has been performed but costs the organism performing it in terms of reproductive success (Trivers, 1974). Hence, although accounting for many behaviors and morphological differences, Darwin failed to explain altruism in terms of natural selection. He could not explain how the behavior, which is reducing one’s fitness, is present in one or another way in organisms. He could not construct the frame in which he could show how altruism increases one’s fitness. Hamilton gave this frame for altruism in 1963. He explained fitness not only in terms of leaving number of surviving offspring but also in terms of increasing total number of genes left behind in the gene pool of the next generation. He explained that the trait, behavior, or variation should benefit the genes rather than merely benefiting the holder. The behavior should add a handful of genes with a higher concentration of specific genes to the gene pool of next
Thereby an organism can increase their fitness not only by producing offspring but also by increasing the proportion of its genes through the means of related individuals. Hamilton coined the term ‘inclusive fitness’ that includes the classical fitness gained through direct reproduction and the proportion of genes gained through related individuals. He explained the evolution of behavior by considering the effect of that behavior on the inclusive fitness of the individual. To perform an altruistic act and to its have survival value for a relative, its benefit/cost ratio has to be larger than the inverse of the altruist’s degree of relatedness to that relative. These costs and benefits have been defined in terms of reproductive success. Hence, by doing an altruistic act, an organism is simply contributing to its genes by taking the risk of reducing its fitness in the ratio of genes it shares with that individual (Hamilton, 1963). For instance, Hymenoptera community such as the society of ants, bees, wasps, etc. which often lives in large colonies and have a very complex social organization, where workers help sister queen to reproduce at the cost of their reproducing ability. However, altruism is not limited to the closely related individuals. Altruistic act benefits distantly related organism as well as members of different species. Taking one more step ahead, Trivers (1971) explains altruism in individuals, which are not closely related even at the level of different species. He sees the altruistic act in terms of reciprocity. According to Trivers, it is the exchange that supports such altruism. Altruistic acts are performed on the unequal cost/benefit ratio of the altruistic act. That is when the cost (the degree to which behavior retards the reproduction of the genes of the altruist) to the performer is trivial as compared to the benefit (degree to which the behavior increases the rate of reproduction of the genes of the recipient) of the recipient and recipient may not be closely related. However, performer expects reciprocity in future when the situation might be reversing (Trivers,
1971). For example, alarm call of a deer or a monkey mutually benefits each other. Human society is the best example of reciprocal altruism, where people often help unrelated individuals. Hence considering all three theories it can be seen that any morphological or behavioral difference is the result of evolution. It includes even the simplest instinctual behavior like eating to as complex as altruism.

**PI, reproductive success, and sexual selection**

PI is prevalent across the animal kingdom. Some taxa show intense PI (almost lifetime involvement, e.g. humans) whereas some taxa show the minimal contribution that is restricted only to the production of sex cell or egg, provisioning of gametes, etc. The form, degree, and intensity of PI vary a lot across taxa. For instance: most of the of Avian and Mammalian taxa show intense parental care due to pre and postnatal care such as gestation, incubation, egg guarding, brood carrying, lactation, feeding, protection. Whereas, in most of the reptiles, fishes, amphibians parental care is not very complex and often it is not even mandatory. Patterns and intensity of PI also differ on the sex of offspring. The role and proportion of investment in the offspring by different sex also differ a lot across different taxa.

PI and sexual selection make a vicious circle affecting each other. PI is an evolutionary strategy that appears to be significantly affected by sexual selection. There is usually competition among the individuals of the same sex, especially males, for reproduction. In the process of sexual selection, those variations are preserved which might be the result of natural selection but giving the advantage of producing more offspring than the other members of same sex and hence increasing their reproductive success. Darwin has explained how members of same-sex compete to get access to opposite sex (Darwin, 1871). In this process of sexual selection explained above, many behavioral and morphological difference emerges which we often call
sexual dimorphism. There is one important factor which affects, which sex will compete and which will select or both will have fair chance to select or to be selected. Relative PI of each sex in their offspring governs it. Trivers (1972) defined PI as, “Any investment by the parent in an individual offspring, that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring”.

It includes investment in sex cells, prenatal development to the stage where offspring becomes capable of surviving on its own. Investment can be made at different stages of the development of offspring and can be described in terms of allocating resources such as time, energy, etc. Trivers excluded any effort made by sexes in finding mates from PI (Robert, 1972). The central idea of Trivers was the proportion of investment made by male and female and the likelihood of desertion by either sex. The cost of PI differs a lot between male and female across the animal kingdom and so is the likelihood of desertion. He assumed total PI as the sum of PI in each of the offspring per season, which can further be divided by the number of offspring produced in the season to get the investment made by a parent for each offspring. The total number of offspring produced each season should be equal for both the sexes. Hence, if the PI of any sex exceeds that of other sex, then the investing sex becomes the limiting resource. This will result in competition among the member of opposite sex to access limiting sex. He divided species based on their relative PI. Species where limiting resource is the female sex (female PI exceeds that of male) then male competition can be seen for example most of the mammals shows male competition and female choice and are a good example of polygamy. Likewise, when a male becomes the limiting source that is males PI exceeds female PI then the opposite can be seen, where females compete to access male, for instance, many birds
have polyandry societies where female competition is seen. However, if the male–female investment is comparable their reproductive success can be expected to vary in similar ways without any discrimination of female or male choice. These differences in PI result in sexual dimorphism and favor different form of societies. It means at any given point if there is any chance of desertion then the sex who has invested least until the moment will be more likely to desert. Hence male and females adopt different parental strategies. Even though most of the Trivers assumptions were accepted, he was opposed on the ground that it is not what a parent has invested until the moment in the offspring, but it is the future prospectus, which governs continuing relative PI by sexes or the likelihood of desertion. The number of offspring an individual can produce after deserting the present will be favored (Dawkins & Carlisle, 1976; Smith, 1977).

Smith (1977) has given pre-copulatory investment as an important factor influencing the number of surviving offspring and finally affecting the fitness of an individual. He explains the importance of pre and post-copulatory efforts in PI with certain conditions. He used and gave the names to the different evolutionary stable strategies explained in Trivers (1972) and Dawkins and Carlisle (1976) model. The two alternative strategies are ‘duck’ strategy, where male deserts the female or invest less in offspring resulting in polygamy and ‘stickleback’ strategy where female deserts the male resulting in polyandry. These two strategies are likely only if one parent can raise the offspring as efficiently as two and the parent who deserts has good chances of getting another mate. This is possible only when there is an excess of one sex and timing of deserting is such that prospects of getting another mate are higher. If there is an excess of female sex, then male competition and desertion by male sex can be seen, whereas if there is an excess of male sex and probability of a
female is higher to get another male for re-mating, then female desertion is likely. However, if the two parents can raise twice as many offspring than single parent and chances to get another mate are little then rather than ‘duck’ or ‘stickleback’ strategy monogamy is seen, where both parents invest in the young (Smith, 1977).

Explanation of these strategies and models that we have discussed has somewhere taken the base of a classic experiment done on *Drosophila melanogaster* by Bateman (1948). In his experiment, he revealed three interesting facts about the sexual differences and reproductive variance of male and female. (i) Reproductive success of male varies a lot as compared to female reproductive success. Male invest little energy in their sex cells as compared to females, hence the reproductive success of female is limited by the number of sex cells or eggs it can produce. Whereas, males reproductive success is limited by the number of eggs it can fertilize rather than the number of sex cells or sperms it can produce. Hence, (ii) male reproductive success is limited by the number of females it can attract, whereas females reproductive success seems to be unaffected by the number of males it can attract. (iii) Reproductive success of female does not increase with the number of times a female copulates but males’ reproductive success increases drastically with a number of time and females it copulates.

Hence, in all the models, where female parental care and investment is a limiting resource for that particular species, the reproductive variance is expected to vary as explained by Bateman (1948). However, species, where male parental care and investment is limiting resource, opposite patterns can be expected. In monogamous species, reproductive success of male and females are expected to vary in a similar way (Bateman, 1948).
Paternal PI

Paternal investment is a set of male care behavior that influences the reproductive success of males. (Dawkins & Carlisle, 1976; Kurland & Gaulin, 1984; Lancaster & Lancaster, 1983; Robert, 1972; Smith, 1977). It is prevalent in most of the species of birds, fishes, and even in some species of insects and few species of mammals, mostly land carnivores and some primates (for e.g. Perrone Jr & Zaret, 1979; Thornhill, 1976; Wolf et al., 1988). The extent of male care across different primate species may vary from extensive and intense care to no involvement at all (Dammhahn & Kappeler, 2005; Dunbar, 1984; Kleiman, 1985; McGrew, 1988; Rosenbaum, Silk, & Stoinski, 2011; Santos, French, & Otta, 1997; Sekulic, 1983; Van Schaik & Van Hooff, 1996; Whitten, 1987; Wright, 1990). There are many theories on the evolution of male care that have attempted to differentiate between male care and paternal investment (Dawkins & Carlisle, 1976; Kurland & Gaulin, 1984; Lancaster & Lancaster, 1983; Robert, 1972; Smith, 1977), which are often used interchangeably (Sheldon, 2002). Male care refers to a set of behaviors directed towards the infant with unknown genetic paternity (Huck & Fernandez-Duque, 2013), whereas, paternal investment involves influencing reproductive success of the male (Robert, 1972). Male care includes two categories of behaviors: Direct care and indirect care. Direct care refers to behaviors such as carrying, holding, grooming, and protection directed towards a particular infant. Indirect care refers to behaviors that benefit infants but are not directed towards them (e.g., defending territory, chasing predators, etc) (Kleiman & Malcolm, 1981). There are multiple justifications of male care because it brings many advantages to males exhibiting it. Males often exhibited care to increase future mating prospects with infant’s mother (Marlowe, 2000; Smuts & Gubernick, 1992) on the one hand and may also use infants merely as a buffering
agent to communicate with other males on the other hand (Ali, 1981; Taub, 1984). However, when male care is exhibited selectively to their offspring and shows at least some amount of paternity certainty, then it is called paternal investment (Alexander et al., 1979; Anderson, 2006; Barash, 1982; Kurland & Gaulin, 1984; Robert, 1972).

Paternal investment can be obligatory or facultative (Arnold & Owens, 2002; Clutton-Brock, 1991; Fishman et al., 2003). It is obligatory in the species where paternal investment is mandatory for the survival of offspring and hence it is selected for. In such species, the male shows a high level of paternal investment (Westneat & Sherman, 1993). In some species, paternal investment is more because of proximate causes and paternity certainty and not mandatory for the infant’s survival. Such PI is categorized as a facultative paternal investment (Westneat & Sherman, 1993).

Most of the mammalian species are dimorphic. Internal fertilization and lactation favor maternal investment than paternal investment, but investment does not end with investment in sex cells and prenatal period. After birth investments are also crucial for the survival of offspring. Hence, in spite of pregnancy and lactation which constrains most of mammalian father’s involvement, male primates show infant care and intense paternal investment across different species (Dammhahn & Kappeler, 2005; Dunbar, 1984; Kleiman, 1985; McGrew, 1988; Rosenbaum et al., 2011; Santos et al., 1997; Sekulic, 1983; Smiseth et al., 2014; Van Schaik & Van Hooff, 1996; Whitten, 1987; Wright, 1990). Paternal investment is very prevalent among bird (Arnold & Owens, 2002; Cockburn, 2003, 2013) and most of the studies are of birds and fish, where male parent also invest in the form of provisioning and carrying. Hence paternal investment is often measured in terms of provisioning and carrying which are uncommon behaviors in male primates. Instead, among primates parental care is exhibited in the form of grooming, defending, playing, huddling and providing
a safe zone for feeding and resting, which benefits infants and improves their survival (Kleiman & Malcolm, 1981). For example, *Cercopithecine* primate species provide adult male care for infants and juveniles in the form of grooming, carrying, and support in agonistic interactions and provide protection against infanticide (Smuts & Gubernick, 1992).

**Maternal PI**

Maternal investment is very prevalent in the animal kingdom. Among mammals, it is much higher as compared to other classes. For instance, 81% of bird species show biparental care (Arnold & Owens, 2002; Cockburn et al., 2016). Hence, it can be expected that among species in which reproductive variance is higher among sexes, the mother might exhibit bias in response to her environmental, social and individual conditions.

*Sex ratio adjustment and maternal PI*

In mammals, reproductive success of males and females varies a lot. Males’ investment in sex cell is negligible as compared to female sex investment in the egg. And not only in egg but females also invest heavily in pre and postnatal stages of infant development at the cost of her somatic maintenance. This high cost makes female desertion very unlikely. Taking the heavy cost of female investment into consideration, it can be expected that, it will be adaptive for a female to adjust the sex ratio of the offspring in response to her own as well as environmental and social conditions, which ultimately affects her bodily conditions.

*Age of females and maternal investment*

Data on age of female and patterns of maternal PI shows much variation among different primate species. This may be because in some species age and rank covary. In many species, male (more costly sex) and females (less costly sex) cost of
rearing varies considerably. As a result, primiparous female (first-time mother) are often relatively inexperienced in directing resources to the young as compared to multiparous females. Hence, producing a daughter, which is usually considered as less costly sex might be of advantage due to a higher chance of mortality in case of costly sex (son) because of insufficient and less experience of directing resource and protecting the sex, for instance, callitrichids. On the other hand, if the cost of rearing both the sex is comparable then there might not be any preference for any sex (Bercovitch, 2002; Bercovitch et al., 1998; Kunkele & Kenagy, 1997). For instance lesser mouse lemurs (Perret, 1990), Muriquis (Strier, 1996), rhesus macaques (Bercovitch et al., 1998; Small & Hrdy, 1986), ring tailed (Nunn & Pereira, 2000). Although most of the species do not seem to be affected by age, some species show the interaction of age and dominance. For example, young subordinate females in savanna baboons produces more males and old dominant females also shows males biased sex ratio (Packer et al. 2000).

Proximate mechanism and maternal investment

To understand the complexity and proximate causes of sex ratio adjustment, it is beneficial to start with reptiles, insects etc. For instance, in many alligators and turtles, sex of the offspring is not the result of sex chromosome typing rather it is a result of incubation temperature (Bull, 1980). Similarly, some insect societies can also control sex ratio through temperature. Many hymenoptera societies which are haplodiploid, queen (fertile female) has the ability to directly control the sex of offspring by fertilizing or not fertilizing eggs (Hamilton, 1967). Even though some species reflects the very clear mechanism of sex ratio adjustment, there has not been any solid evidence for the prevalence of any physiological or behavioral mechanism showing adjustment or modification of sex of the offspring at the time of conception in the
case of primates and even mammals (Bercovitch, 2002). However, mammalian testosterone has shown to be influenced by environment which in turn can influence birth sex ratio (Gray, 1992; Kemper, 1990; Mazur and Booth, 1998; Rose et al., 1971). From the time binomial distribution of sex ratio was disclosed, some considered it as the support of facultative adjustment of sex ratio, whereas others considered it as the mechanism of non-modification (Gowaty, 1991; Williams, 1979). Hence, it can be inferred that proximate mechanism of sex ratio does exist in lower order animals. However, reproductive complexity makes it difficult to identify these mechanisms in higher order animals.

Local Resource Competition

This model considers the local resources and environmental conditions and expects variation in the sex ratio. It takes maternal conditions as the proxy of maternal rank and explains the variation in sex ratio. Most of the group living species shows dominance hierarchy which directly influences their position in the group and also characterizes female philopatry (females remains in the natal group, whereas males migrate). In the case of females, this mainly means priority of access to food, shelter, and protection. Hence, females can be divided based on their rank, and different rank females may adopt different strategy depending on resources and the environment. Hence, under intense local resource competition high-rank females are expected to produce more daughters, because daughter can help them in maintaining their status and can support them in conflicts. As a result, this increases access to the resource rather than having as on. However, low-rank females may benefit from producing sons because it might be difficult for low-rank females to protect their daughter from harassment from unrelated high-rank females. When resource competitions are relaxed opposite patterns can be expected. The producing son may be advantageous

**Trivers-Willard hypothesis**

According to Trivers and Willard (1973), parental conditions affect the sex ratio of their offspring at the time of birth. They state that maternal health condition during the period of PI will be associated with the health condition of offspring at the end. In sexually dimorphic species, where the reproductive success of male and female varies considerably (Robert, 1972) natural selection will favor adjusting sex of offspring in response to mother’s condition. Hence, “good parental conditions” will be associated with the conception of male offspring and vice-versa (Trivers & Willard, 1973). A healthy female’s offspring, if it is a male, would also be healthy and would sire more offspring, thereby increasing her inclusive fitness. On the other hand, a weak female should produce a daughter since all females, regardless of their physical strength, end up reproducing.

**PI in reptiles, amphibians, fishes and insects**

Post-partum and post-oviposition parental care in the reptiles, amphibians, fishes, and insects is not as prevalent as it is in mammals and birds. Parental care is very uncommon among insects and amphibians. In most of the species, prepartum care is present in the very primitive form of supplying egg with small amount of yolk; however, some species show post-partum parental care too. For instance, in treehopper *Publilia concave* (Zink, 2003). Royle et al. (2012) stated that the parental care should include both behavioral as well as morphological traits if they serve the similar function of caring for infant. He defined parental care in broader terms and explained it as any parental trait, which is originated or maintained to provide fitness benefit. Parental care in these taxa is prevalent in the very primitive form of gamete
provisioning, viviparity, ovoviviparity, oviposition site selection, nest building and burrowing, egg attendance, egg brooding, offspring attendance, food provisioning (Royle et al., 2012). Many insects provide resource to the eggs to protect them from environmental hazards such as desiccation, drowning, predators, and pathogens (Zeh et al. 1989). Females’ insects also enhance their fitness through ovipositing (laying eggs non-randomly) (Refsnider & Janzen, 2010). Even though post-partum care is generally rare in reptiles, some species of lizard shows post-partum care such as black rock skinks (Egernia saxatilis) to prevent infanticide (O’Connor & Shine, 2004), female Eumeces and Ophisaurus brood their eggs and E. obsoletus remains with the young even after hatching of eggs for ten days (Smith, 1977). In the amphibians, parents increase the chances of survival of offspring by carrying eggs and tadpoles throughout the development and metamorphosis, by providing eggs to their tadpoles, have internal gestation within oviduct, transfer tadpoles from terrestrial oviposition to water, etc. (see Crump, 1996). Fishes show a different spectrum of PI. PI varies in fishes from simple egg burrowing to internal gestation to live bearing. Even though fishes involve all three kinds of PI from male and female alone investing into the infant to both sexes working together, male parental care predominates in fishes (Gross & Sargent, 1985) for instance bony fish (Blumer, 1979).

**PI in birds**

Birds are different from mammals due to lack of lactation, whereas it is distinct from lower vertebrates because it’s reproductive success is not limited by the number of egg a female can lay, rather it is limited by the number of eggs it can incubate or number of offspring it can feed. Hence, PI after laying of egg is more important in birds (Lack, 1968). Unlike mammals, where gestation and lactation favor female PI, birds have tremendous opportunities for both male and female parental
care as well as chance of desertion by either sex (Smith, 1977). Hence, most of the birds are monogamous. Almost 75% of birds exhibit biparental care in known species, whereas inferred for 81% species of birds. Only 1% of bird species that is approximately 90 species of birds shows exclusively male parental care. Female parental care is exhibited among almost 772 species, almost in 8% of species. Other species show either cooperative breeding or no parental care (Arnold & Owens, 2002; Cockburn, A., 2013; Cockburn et al., 2016).

**PI in mammals**

Most of the mammalian species are dimorphic. The female sex invests large amount of energy in its sex cell, prenatal period, and postnatal period because of gestation and lactation. Male’s sex cells are quite small as compared to that of the female, and they invest very little amount of energy in the production of these cells. Male PI and care is very uncommon among mammals. However, in some land carnivorous animals, male feeds the young, whereas herbivorous and fish-eating mammals do not seem to follow this. Males also provided protection to their young ones in some species. However, rare but extensive male care is also prevalent in mammals (Dammhahn & Kappeler, 2005; Dunbar, 1984; Kleiman, 1985; McGrew, 1988; Rosenbaum et al., 2011; Santos et al., 1997; Sekulic, 1983; Van Schaik & Van Hooff, 1996; Whitten, 1987; Wright, 1990). Hence, in most of the species, male competition and female choice is predominant. Among mammals also primates show the potential to prolong their investment almost for lifetime as long as they share the same habitat (Fairbanks, 1988, 2000). Unlike most of the mammals, which provides direct care such as nursing, feeding, carrying, etc. to the offspring, primate mothers also provide “umbrella” care, which is shared among siblings. This extended social or
umbrella care provides offspring learning opportunities, protection against predators and agonistic encounters (Van Noordwijk, 2012).

**Dominance hierarchy**

Dominant and subordination are the results of competitions over resources. Winner of successive encounters over resources such as food, mate, etc. is usually called dominant, and the one who loses is referred as a subordinate. Hence, dominance is state or condition that gives priority of access to the resources available (Clutton-Brock et al., 1986; Timothy et al., 1977; Gauthreaux, 1978; Morse, 1974; Popp & DeVore, 1979; Syme, 1974; van Kreveld, 1970; Wagner & Gauthreaux, 1990; Wilson, 1975; Wolfe, 1984). From these successive encounters between individuals of the same group, hierarchy of dominant, and subordinate, emerge. By the very definition, dominance gives priority of access to resources available that includes mate too. Dominant animals gain differential access to members of opposite sex hence reproduces more offspring than others (Alberts et al., 2006; Altman et al., 1996; De Ruiter and Van Hooff, 1993). Mostly, in context to male, dominant male sires more offspring. However, in females dominance provides priority of access to food, security, etc., and hence influencing female condition both in a direct and indirect way influencing offspring position in-group and her reproductive success.

**Dominance hierarchy, expected PI patterns, and contradictory empirical data**

The focus of the present study is the most debated ‘Trivers and Willard hypotheses’ of sex ratio biases. Literature is full of the attempts in describing difficulties in sustaining Trivers and Willard hypothesis, but the manipulation of the sex ratio by parent remains a central part of successful reproductive strategies. According to Grant’s maternal hypothesis (2003), ‘Women dominant in personality as compared to the other women are more likely to conceive male infant’. Correlation
between dominance and serum testosterone level has been found (Grant, 2003; Mazur & Booth, 1998; Rose et al., 1971). The maternal dominance hypothesis offers serum testosterone as a primary candidate. However, environment influences mammalian testosterone (Gray, 1992; Kemper, 1990; Mazur & Booth, 1998; Rose et al., 1971). Thus, there must be proximate causes or psychoneuroendocrinological systems, which can play a role in interpreting the existing condition and varying testosterone level in response to environmental factors that in turn can affect the sex of ratio of offspring (West & Sheldon, 2002). These conditions are correlated with dominance, whereas dominance systems themselves are determined by the life-history traits, individual development, behavior, perception, and cognition (Pereira, 1995). There is a typical systems of agonistic interactions built around this social dominance, which we often use as a means of measuring dominance strength. Dominance enhances superiority of access to resources and lessens inferior rates and effects of aggression received, thus increasing individual survival and reproduction (Allee, 1938; Tinbergen, 1953).

According to parental condition, adaptive variation in sex ratio has been reported for birds (Clutton-Brock, 1986; Gowaty, 1993), ungulates (Hewison & Gaillard, 1999), other mammals (Gowaty, 1993; Hewison & Gaillard, 1999; West & Sheldon, 2002) and in primates (Brown, 2001).

Since the times of Bateman (Bateman, 1948; Bateman effect), it is an established fact that reproductive variance among males is higher than females. In higher organisms such as Primates, where almost all females reproduce with little variance, dominant males sire significantly higher number of offspring than subordinate males. Males’ reproductive success does not seem to be limited by the number of sex cells produced but by the number of eggs fertilized by these cells because in terms of energy investment males’ sex cells require too little metabolic
energy. On the other hand, females invest a good amount of energy. Hence, the number of egg cells a female can produce controls her reproductive success. Trivers (1972) has assumed that in polygyny, sexually dimorphic species, because of higher variance in male reproductive success than female, maternal investment influences male reproductive success more as compared to females (Trivers, 1971). For instance, Clutton-Brock et al. (1984, 1986) and Kruuk et al. (1999) have reported in red deer (Cervus elaphus) that maternal dominance rank does affect males’ reproductive success but not female reproductive success. Further, it has also been reported that in species where dominance is unambiguous and more towards linearity, mother’s rank can influence the status of offspring such that the offspring of a dominant female tends to gain a higher social rank (Kawamura, 1958). However, this topic of sex ratio variation has remained controversial. Brown and Silk (2002) have suggested that still we cannot conclude whether maternal rank and condition does influence sex ratio. There are as many publications against as in support of the hypothesis that dominance affects sex ratio. Many attempts have been made to study the effect of maternal rank on sex ratio but only a few attempts have been made for looking at after birth investment patterns in relation to sex of offspring. It can therefore be hypothesized that a dominant female should invest more in the son who as dominant male would get the female a larger number of grand-offspring and hence increase her inclusive fitness. On the other hand, subordinate females should invest more or with no difference in daughters who would reproduce as adults anyway whereas their sons becoming subordinate males may not get chances to reproduce. Since in mammals, a female continues to invest heavily in the offspring feeding milk, the investment on the “appropriate” sex of the offspring can be appreciated during the period of birth of the offspring and weaning. Although these predictions have been attempted to be verified
in some species, there is no conclusive data on the dominance status of the females and their PI patterns. Such data on males are almost entirely absent.

**Dominance hierarchy and PI patterns in lion-tailed macaques – a non-seasonal breeder**

A study by Singh et al. (2007) on lion-tailed macaque (*Macaca silenus*) in the Western Ghats of India found that high-ranking females made more PI on their male offspring than their female offspring. Whereas the lower ranking females either did not show sex bias in PI or the bias was towards female offspring. One of the ways in which the dominant females made extra investment on their male offspring was to prolong the milk feeding by delaying weaning resulting in a longer inter-birth interval (IBI) for producing the next offspring. Lion-tailed macaques are largely non-seasonal breeders (Sharma et al., 2006) and a female can afford to delay weaning as mating can occur at any time of the year for next reproduction.

**Expected PI patterns in a seasonal breeder – the bonnet macaque**

However, in species that is strictly seasonal breeder, such a strategy is not available to the females. The bonnet macaque (*Macaca radiata*) of South India is strictly a seasonal breeder (Sinha, 2001). Mating in this species occurs in July-September, and the infants are born in February-April. It would, therefore, be interesting to see what strategy the bonnet macaques employ and what will be the relationship between dominance status and the PI patterns in the bonnet macaques. The present study has been designed keeping in view the above theoretical perspective. Since male PI in macaques has hardly been studied, it is also proposed to include the study of male PI patterns in this species. Further, unlike most other macaques, the bonnet macaques are usually multi-male groups with a sex ratio of males almost close to that of females (Singh and Rao, 2004). In such a species,
investment on younger infants can be expected to be made by males in order to build future alliance and gaining fitness advantage from living in multi-male groups (Rosenbaum et al., 2011). The present study, therefore, has been designed with the following title:

PATERNAL INVESTMENT PATTERNS IN RELATION TO DOMINANCE STATUS IN BONNET MACAQUE (Macaca radiata)