IJSIR

International Journal of Scientific and Innovative Research 2017; 5(2) : 20 - 27
P-ISSN 2347-2189, E- ISSN 2347-4971

AGING IN INSECTS: AN OVERVIEW

***Kalpana Singh**

Department of Zoology, University of Lucknow, Lucknow, Uttar Pradesh, India

*Address for correspondence : Dr. Kalpana Singh, Assistant Professor, Department of Zoology, University of Lucknow, Lucknow, Uttar Pradesh, India
Email ID: drkalpanasingh@gmail.com

ABSTRACT

Aging can be defined as a decline in rate of physiological repair, an increase in probability of death and a decline in fertility with advancing adult age. It affects virtually all demographic, behavioral and physiological parameters in an individual. Its effect on activity levels and reproductive behaviour such as mate choice are well studied in insects. Reproductive attributes such as fecundity and egg viability are affected by the age of mating pair; however effects of paternal age are less studied. Effects of maternal age on offspring life span are well established in many animal groups (Lansing effect). Many theories have been proposed to explain the causes and evolution of aging; viz. mutation accumulation hypothesis, antagonistic pleiotropy hypothesis, disposable soma theory. Lansing effect may also play an important role in evolution of aging emphasizing the importance of parental age at the time of reproduction.

***Keywords*:** Aging; Mate Choice; AternalAge; Paternal Age; Progeny Fitness

INTRODUCTION

Aging is a function of time over biological systems. It has fascinated the scientists the world over since it affects each and every aspects of life. It still remains a great mystery although systematic efforts have been going on since last century to understand it. It affects the life attributes and physiology of organisms.[1,2,3] All over the biological world only a small percentage of organisms survive in nature that are subjected to age. The effects of aging are much more pronounced in captive populations that live in benign condition.[4,5]Insects being a good model, a lot of base line studies have been conducted on them[6] although there are numerous studies on human beings and other mammals.[7,8,9,10] Since, life span of insects is very short so the genetics and evolution of genetics had predominantly investigated in insects.[6]

Aging has been defined in many ways. As per physiological definition it is a decline of state of repair with increasing age. While actuarial definition states it as an increase in mortality rates of a population with increasing age. As per evolutionary definition it is a persistent decline in components of fitness (rates of survival and reproduction) with increasing age.[11]

Thus, aging can comprehensively be defined as a decline in fertility, a decline in rate of physiological repair and an increase in probability of death with advancing adult age.[11]There are numerous prolonged demographic studies that report aging in the form of an increase in probability of death and decline in fertility with advancing adult age.[12] Its rate may differ and evolve in different organisms although it is recognized that aging is maladaptive.[13]

Keeping in view the universal presence of aging this article aims to review the studies on aging, aging theories, aging rates and aging effects on life attributes in insects.

THEORIES OF AGING

Various theories have been put forward to explain the phenomenon of aging and its causes and evolutionary significance. These theories can be summed up into two categories intrinsic (programmed) and extrinsic (Stochastic).[14] These two types of theories interact also such as in *disposable soma* (extrinsic) theory.

There are many theories that may fall into intrinsic theory category such as *mutation accumulation* hypothesis and *antagonistic* *pleiotropic* hypothesis. *Mutation accumulation* hypothesis states that the aging is caused due to the increase in mutation rates along with the decreasing force of natural selection and this in turn leads to less probability of survival at later ages.[3,15,16] This corroborates with the studies conducted since 1940's where evolutionary biologists have argued that the age related decrease in the force of natural selection leads to evolution of aging.[17,2,3] According to *antagonistic pleiotropic hypothesis* a new mutation that increases fertility and fitness levels at young age at the expense of lowered fitness levels later in life (pleiotropic effect) will be selected.[2,15,16]

Disposable soma theory of aging explains that aging is an environmentally driven balance between investment in reproduction and maintenance of soma.[18] It observes that (i) somatic maintenance has a cost, (ii) maintenance of the soma more than the natural expectation of life is disadvantageous, and (iii) maximum deaths in natural populations is due to extrinsic mortality. This is a physiological ecology based life history optimization theory that somewhere converges with the antagonistic pleiotropy theory of aging.[19,18] According to Heininger(2012)[14] aging is a deprivation syndrome driven by a germ soma conflict. This helps to explain the multiple life history trade-offs occurring in organisms.

The studies conducted on *Drosophila melanogaster* have substantiated the mutation and antagonistic pleiotropy theories of aging.[20,15,21,22] Results of experiments conducted on *D. melanogaster* about age specific genetic variance[23,24,25] & inbreeding depression [26]have corroborated the importance of mutation accumulation in aging. However there are studies on artificial selection experiments that enforce the importance of pleiotropy. Gerontologists have shown great interest in antagonistic pleiotropic studies.[21,27]

EFFECTS OF AGE ON LIFE TTRIBUTES

On Activity Levels

Predator's age have been found to influence rate of predation in ladybird beetle, *C. transversalis* and *C. sexmaculata*. Rate of assimilation and speed of locomotion were also found to decline with increase in age that indicates senescence.[28] Almost all demographic, behavioral and physiological parameters are known to qualitatively deteriorate with the increase in age.[12,29] Reproductive senescence in terms of decrease in fecundity and exhaustion of reserves in adults has been demonstrated in hymenopteran parasitoids,[30]lepi dopterans[31,32,33] & ladybirds.[34]

On Mate Choice

There are many studies that investigate the role of age in the choice of mates in insects. These studies have come out with three various models that explain the behavior of female exerting the age based choice of mates. Few studies suggest that females tend to choose old males as mates and this formulates the good genes model or indicator mechanism.[35,36,37,38]This theory explains that older males have proven their fitness by their long survival thus should be selected.[29,40] There are many studies to substantiate the same.[41,42,43,44,45,46,47] This model suggests that that individuals differ in genetic quality leading to increased survival and fecundity of higher quality individuals at all ages.

However there are some contrary reports.[48,49,50,51,52] Mate choice model put forward by Hansen &Price (1995)[53]presents that females choose younger males as mates.[54,55]They suggest that a trade-off between early and late-life fitness components is likely to lead to such preference.

The third model suggests that female choose middle aged mates.[56,57]

On Mating Incidences

There are many studies that report the effect of aging on mating incidences *i.e.* how many mating does a insect undergoes at different ages. Age specific mating incidences have been recorded in Adaliabipunctata to analyze the phenomenon of protandry and protogyny. [58]The males started mating after 4 days of age while female mated at the age of 2 days in Coccinellaseptempunctata. Age related decrease in willingness to mate and decrease in mating incidences were found after 40-50 days of age in both the sexes of this beetle.[59]In pale morph of Propyleadissecta few younger females have chosen the older males while older females have chosen the older males.[60]

On Male Reproductive Attributes

There are very few studies on insects dealing with effect of paternal (male) age on reproductive fitness of its own or that of females. Studies in ladybirds considering the assessment of paternal age effects on reproductive attributes came out with significant results. Viability of eggs laid was found to be male-age-dependent function. Up to the age of 30 days there was no decline in percent viability in pale morph of *Propyleadissecta*[60]and decline was observed after 30 days in *Coccinellaseptempunctata*[59] and *Cheilomeness exmaculatus*.[61]

The effects of male age and its effects are largely ignored aspect of studies in insects. However Fox *et al*., (1995)[62]dealt with variation in ejaculate size with age and its effect on female fecundity.

On Female Reproductive Attributes

Some lepidopterans exhibit a decline in egg production with increasing age of mother.[63,64,65,66,67,68] Decline in egg size with advancing maternal age have been reported in butterflies that lay their eggs singly.[69,70,71,72]In braconid *Micro plitscroceipes* (Cresson),[73]chalcid, *Brachy-meris inter media* (Nees)[74] and Female moth *Epi-phyaspostvittana* (Walker)[75] showed decreasing fecundity and fertility with increasing age.

In ladybeetle, *C. montrouzieri* fecundity was significantly affected by the age of female, as 5 to 15-day-old females laid larger number of eggs.[76]In ladybirds *C. septempunctata* and *P. dissecta*(pale morph) fecundity was affected by the advancing age of the females. Senescence was reported after 20 days in females of both the ladybirds.[60,59]

In *Drosophila melanogaster* it was reported that the last male sperm precedence declined significantly in three strain of the species indicating the start of senescence as physiological deterioration.[77]

Effect of Aging on Offspring Fitness

The younger mother, on the average, had the longest lived offspring-Alexander Graham Bell (1918) . Researchers have found that in insects older mothers have shorter lived offspring in house flies,[78] fruit flies,[79] stink bugs,[81]flour beetles,[82]and mealworms.[83,84] This is referred to as the *Lansing effect*,after Albert Lansing's (1947,1948,1954)[85,86,87]renowned work on rotifers.

In *C. montrouzieri* the female age had non-significant effect on development of grubs.[76] However in fruit flies it was reported that delayed mating of mothers had affected the rate of recombination and non-disjunction in their offspring.[88]In *Brachymeriaintermedia* (Nees) maternal age controls itspopulation growth.[89]

Priest *et al.,*(2002)[90] reported that age of mother had affected the longevity of her offspring. In the wild caught strain of *D. melanogaster* age of mother had affected the male progeny life expectancy. It was found that mothers which reproduced continuously throughout their life have offspring with higher life expectancy than the mothers with delayed reproduction. The results show that maternal age affects the patterns of aging of offspring.

A single study in ladybirds demonstrates that the age of parental generation affects the reproductive parameters of progeny thus playing critical role in determining fitness of future generations.[91]

CAUSES AND EVOLUTION

Kirkwood (2002)[10] explains aging with the disposable soma theory that tells that aging is a balance between investment in reproduction and maintenance of soma which is also environ-mentally modulated. Whereas, Heininger (2012)[14] has explained aging as a deprivation syndrome driven by a germ soma conflict.

The Lansing effect predicts that the older mother produce short lived offspring. This effectmay also have asignificant role in the evolution of aging. Natural selection may also operate on the offspring produced by parents of different ages thus influencing the evolution of aging provided the effect of parental age on offspring longevity varies among different genotypes.

There are many studies that show that longevity and survival of the organisms including insects depends on their sexual activity in males and reproductive efforts in terms of mating, oviposition in females.[92,93,94,95,96]

Life history evolution for understanding the mechanism of aging has been explained by resource allocation models. This model postulates that there is a trade-off between different life history traits and reproduction is costly and often results in either lowered fecundity or survival . [1,97,98,99,100,101] This trade-off is well studied in Arthropoda especially in insects.[20,94,102,27,103]

Increased reproduction is costly as it may lead to reduced longevity. In female insects it is expressed as purely phenotypic effects[35,102] or as additive genetical effects.[104] It is very well demonstrated in *D. melanogaster.*[92]

ACKNOWLEDGEMENT

The author is grateful to the Head, Department of Zoology, University of Lucknow, Lucknow, Uttar Pradesh, India for providing necessary laboratory facilities.

REFERENCES

1. Fisher, R. A. The Genetical Theory of Natural Selection. Oxford: Clarendon Press. (1930).
2. Williams, G.C. Pleiotropy, natural selection and the evolution of senescence. Evolution. (1957); 11: 398-411.
3. Hamilton, W.D. The molding of senescence by natural selection. Journal of Theoretical Biology. (1966); 12:12-45.
4. Ricklefs, R.E. Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. The American Naturalist.(1992); 152:24-44.
5. Wachter, K.W. & Finch. C.E. Between Zeus and the Salmon. The Biodemography of Longevity. National Academy Press. (1997).
6. Arnqvist, G. & Nilsson, T. The evolution of polyandry: multiple mating & female fitness in insects. Animal Behavior.(2000); 60: 145-164.
7. Finch, Caleb E.; Tanzi, Rudolph E.Genetics of Aging. Science. (1997); 278, (5337), p. 407 (1997).
8. Kirkwood, T.B.L. &Austad, S.N. Why do we age. Nature.(2000); 408: 233-238.
9. Kirkwood, T.B.L. Human senescence. BioEssays.(1996); 18:1009-1016.
10. Kirkwood, T.B.L. Evolution of ageing. Mechanisms of Ageing Development.(2002); 123:737-745.
11. Mangel, M. Complex adaptive systems, aging and longevity. Journal of Theoretical Biology.(2001); 213:559-571.
12. Finch, C.E. Longevity, Senescence and the Genome. University of Chicago, Press.(1990); pp. 922.
13. *Medawar*, P.B. An Unsolved Problem of Biology. H. K. Lewis, London. (*1952*).
14. Heininger K. The Germ-soma Conflict Theory of Aging and Death: Obituary to the "Evolutionary Theories of Aging". Webmed Central AGING (2012); 3(4):WMC003275 doi: 10.9754/ journal.wmc.2012.003275
15. Partridge, L. & Barton, N.H. Optimality, mutation and the evolution of aging. Nature.(1993); 362:305-311.
16. Pletcher, S.D. and Curtsinger, J.W. Mortality plateaus and the evolution of senescence: why are old-age mortality rates so low? Evolution. (1998); 52: 454-464.
17. Medawar, P.B. Old age and natural death. Mod. Q. (1946); 2:30-49.
18. Kirkwood T. B. L. and Rose, M. R. Evolution of Senescence: Late Survival Sacrificed for Reproduction. In, The Evolution of Reproductive Strategies (1991); pp. 15-24
19. Kirkwood, T. B. L. Evolution of ageing. Nature, Lond. (1977); 270, 301-304.
20. Rose, M. Laboratory evolution of postponed senescence in *Drosophila melanogaster*. Evolution.(1984); 38:1004-1010.
21. Zwaan, B., Bijlsma, R. & Hoekstra, R.F. Direct selection on life span in *Drosophila melanogaster*. Evolution. (1995); 49: 649-659.
22. Charlesworth, B. & Hughes, K.A. Age specific inbreeding depression and components of genetic variance in relation to the evolution of senescence. Proceedings National Academy of Sciences, USA. (1996); 93:6140-6145.
23. Hughes, K.A. &Charlesworth, B. A genetic analysis of senescence in *Drosophila*. Nature.(1994); 367:64-6611.
24. Promislow, D.E., Tatar, M., Khazaeli, A.A. &Curtsinger, J.W. Age-specific patterns of genetic variance in *Drosophila melanogaster*. I. Mortality. Genetics. (1996); 143: 839-848.
25. Tatar, M., Promislow, D.E.L., Khazaeli, A.A. &Curtsinger, J.W. Age-specific patterns of genetic variance in *Drosophila melanogaster*. II. Fecundity and its genetic covariance with age-specific mortality. Genetics. (1996); 143: 849-858.
26. Charlesworth, B. & Hughes, K.A. Age specific inbreeding depression and components of genetic variance in relation to

the evolution of senescence. Proceedings National Academy of Sciences, USA. (1996); 93:6140-6145.
27. Partridge, L., Prowse, N. &Pignatelli, P. Another set of responses and correlated responses to selection on age at reproduction in *Drosophila melanogaster*. Proceedings Royal Society of London. Part B. Biological Sciences. (1999); 266: 255-261.
28. Dixon AFG, Agarwala BK. Triangular fecundity function and ageing in ladybird beetles. Ecological Entomology. (2002); 27:433–440.
29. Rose, M. Evolutionary Biology of Aging. Oxford University Press. Oxford, New York.(1991).
30. Fernando, L.C.P. & Walter, G.H. Activity patterns and oviposition rates of *Aphytislignanensis*females, a parasitoid of California red scale *Aonidiellaaurantii* implications for successful biological control. Ecological Entomology.(1999); 24:416-425.
31. Dunlap-Pianka, H., Boggs, C.L. & Gilbert, L.E. Ovarian dynamics in Heliconiine butterflies: programmed senescence versus eternal youth. Science. (1977); 197:487-490.
32. Boggs, C.L. Reproductive strategies of female butterflies: Variation in and constraints on fecundity. Ecological Entomology. (1986); 11:7-15.
33. Boggs, C. L. Resource allocation in variable environments: Comparing insects and plants. (F. Bazzaz and J. Grace, Eds.) Plant Resource Allocation. Academic Press. (1997); 73-92.
34. Blackman, R.L. The effects of different aphid foods on *Adaliabipunctata* L. and *Coccinella septe-mpunctata* L. Annals of Applied Biology. (1967); 59:207-219.
35. Trivers, R.L. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man-1871-1971 (ed. B. Campbell.) Chicago 1L: Aldine Press. (1972); P. 136-179.
36. Halliday, T.R. Sexual selection and mate choice. In: Behavioral Ecology: An Evolutionary Approach (eds. Krebs, J.R. & Davies, N.B.). Blackwell Scientific Publishers, London. (1978); P. 180-213.
37. Halliday, T.R. The study of mate choice. In: Mate choice (ed. P. Bateson). Cambridge University Press. Cambridge.(1983); P. 3-32.
38. Manning, J.T. Choosy females and correlates of male age. Journal of Theoretical Biology.(1985); 116:349-354.
39. Kokko, H. & Lindstrom, J. Evolution of female preference for old mates. Proceedings of the Royal Society of London, Series B. (1996); 263:1533-1538.
40. Kokko, H. Good genes, old age and life-history trade-offs. Evolutionary Ecology. (1998); 12:739-750.
41. Burley, N. Mate choice by multiple criteria in a monogamous species. The American Naturalist. (1981); 117:515-526.
42. Grant, B.R. & Grant, D.P.R. Mate choice in Darwin's finches. Biological Journal of the Linnean Society.(1987); 32:247-270.
43. vanRhijn, J. &Groothius, T. On the mechanism of mate selection in black-headed gulls. Behaviour.(1987); 100:134-169.
44. Conner, J. Older males have higher insemination success in a beetle. Animal Behavior. (1987); 38: 503-509.
45. Poole, J.H. Mate guarding, reproductive success and female choice in African Elephants. Animal Behavior.(1989); 37:842-849.
46. Hasselquist, D., Besch, S. & von Schantz, T. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature.(1996); 381:229-232.
47. Sundberg, J. & Dixon, A. Old, colourful male yellow hammers, *Emberizacitrinella*, benefit from extra-pair copulations. Animal Behavior.(1996); 52:113-122.
48. Berven, K.A. Mate choice in the wood frog, Ranasylvatica. Evolution. (1981); 35:707-755
49. Alatalo, R., Gustafsson, L. & Lundberg, A. Do females prefer older males in polygynous bird species? The American Naturalist. (1986); 127:241-245.
50. Koenig, W.D. Levels of female choice in the white-tailed skimmer *Plathemislydia* (Odonata: Libelluliade). Behaviour. (1991); 119:193-224.
51. Petrie, M. Do peacock's trains advertise age? Journal of Evolutionary Biology. (1993); 6:443-448.

52. Olsson, M. & Madsen, T. Female choice or male quantitative traits in lizards- Why is it so rare? Behavioral Ecology and Sociobiology. (1995); 36:179-184.
53. Hansen, T.F. and Price, D.K. Good genes and old age: do old mates provide superior genes? Journal of Evolutionary Biology.(1995); 8:769-778.
54. Alatalo, R., Gustafsson, L. & Lundberg, A. Do females prefer older males in polygynous bird species? The American Naturalist. (1986); 127:241-245.
55. Price, D.K. & Hansen, T.F. How does offspring quality change with age in male *Drosophila melanogaster*? Behavioral Genetics. (1998); 28: 395-402.
56. Beck, C.W. & Powell, L.A. Evolution of female mate choice based on male age: Are older males better mates? Evolutionary Ecology Research.(2000); 2:107-118.
57. Jones, T.M., Balmford, A. &Quinnell, R.J. Adaptive female choice for middle-aged mates in a lekkingsandfly. Proceedings of the Royal Society of London, Series B.(2000); 267: 681-686.
58. Hemptinne, J.L., Dixon, A.F.G. & Adam, B. Do males and females of the two-spot ladybird, *Adaliabipunctata* (L.) differ in when they mature sexually? Journal of Insect Behavior.(2001); 14(3): 411-419.
59. Srivastava, S. and Omkar. Age specific mating and reproductive senescence in seven spotted ladybird, *Coccinellaseptempunctata*. Journal of Applied Entomology. (2004); 128 (6):452-458
60. Pervez, A., Omkar and Richmond, A.S. The influence of age on reproductive performance of a predatory ladybird beetle, *Propyleadissecta*. Journal of Insect Science. USA. (2004); 4 (22): 1-8.
61. Omkar, Singh S. K. & Singh K. Effect of age on reproductive attributes of an aphidophagous ladybird, *Cheilomenessexmaculata*. Insect Science. (2006); 13(4): 301–308, August 2006
62. Fox, C.W., Hickman, D.L., Raleigh, E.L., &Mousseau, T.A. Paternal investment in a seed beetle (Coleoptera: Bruchidae): influence of male size, age, and mating history. Annals of the Entomological Society of America. (1995); 88:101-103.
63. Wellington, W.G. Some maternal influences on progeny quality in the western tent caterpillar, *Malcosomapluviale* (Dyar). Canadian Entomologist. (1965); 97:1-14.
64. Harvey, G.T. Mean weight and rearing performance of successive egg clusters of eastern spruce budworm (Lepidoptera: Tortricidae). Canadian Entomologist.(1977); 109:487-196.
65. Harvey, G.T. Environmental and genetic effects on mean egg weight in spruce budworm (Lepidoptera: Tortricidae). Canadian Entomologist. (1983); 115:1109-1117.
66. Richards, L.J. & Myers, J.H. Maternal influences on size and emergence time of the cinnabar moth. Canadian Journal of Zoology. (1980); 58:1452-1457.
67. Jones, R.E., Hart, J.R. & Bull, G.D. Temperature, size and egg production in the cabbage butterfly, *Pierisrapae* L. Australian Journal of Zoology.(1982); 30:223-232.
68. Murphy, P.A., Giesel, J.T., &Manlove, M.N. Temperature effects on life history variation in *Drosophila simulans*. Evolution. (1983); 37:1181-1192.
69. Wiklund, C. &Persson, A. Fecundity, and the relation of egg weight variation to offspring fitness in the speckled wood butterfly *Parargeaegeria*, or why don't butterfly females lay more eggs? Oikos.(1983); 40:53-63.
70. Karlsson, B. and Wiklund, C. Egg weight variation and lack of correlation between egg weight and offspring fitness in the wall brown butterfly, *Lassiommatamegera*. Oikos.(1984); 43:367-385
71. Karlsson, B. and Wiklund, C. Egg weight variation in relation to egg mortality and starvation endurance of newly hatched larvae in some satyrid butterflies. Ecological Entomology. (1985); 10: 205-211.
72. Wiklund, C. &Karlsson, B. Egg size variation in satyrid butterflies: adaptive vs historical "Bauplan", and mechanistic explanations. Oikos. (1984); 43: 391-400.
73. Navasero, R. and Elzer, G. Influence of maternal age and host deprivation on egg

production and parasitisation by *Micro pletiscroceipes* (Hymenoptera: Braconidae). Entomophaga. (1992); 37: 37-44.

74. Barbosa, P., Martinat, P. & Bennett, R. Consequences of maternal age and host deprivation on the production and development of *Brachymeria inter media* (Nees) and the mortality of its gypsy moth (*Lymantriadispar* L.) host. Journal of Applied Entomology. (1986); 101:215-223.
75. Foster, S.P. & Howard, A.J. The effects of mating, age at mating, and plant stimuli, on the life time fecundity and fertility of the generalist herbivore *Epiphyaspostvittana*. Entomologia Experimentaliset Applicata. (1999);91:287-295.
76. Jalali S.K., Singh S.P. &Biswas S.R. Effect of temperature and female age on the development and progeny production of *Cryptolaemus mon-trouzieri* Mulsant (Coleoptera: Coccinellidae). Entomon. (1999) ; 24: 293-296.
77. Mack, P.D., Priest, N.K. &Promislow, D.E.L. Female age and sperm competition: Last male precedence declines as females age increases. Proceedings the Royal Society of London, Series B.(2002); 270: 159-165.
78. Rockstein, M. Longevity of male and female house flies. Journal of Gerontology. (1957); 12: 253-256.
79. Butz, A. & Hayden, P. Effect of age of male and female parents on the life cycle of *Drosophila melanogaster*. Annals of Entomological Society of America. (1961); 55: 617-618.
80. O'Brian,D. M.Effect of parental age on the life cycle of *Drosophila melanogaster*. Annals of the Entomological Society of America.(1961); 54: 412-416.
81. Kiritani, K. & Kimura, K. Effects of parental age on the life cycle of the Southern green stink bug, *Nezaraviridula*. Applied Entomological Zoology.(1967); 2:69.
82. Raychaodhuri, A. &Butz, A. Effect of paternal age on the life cycle of *Triboliumconfusum* (Coleoptera: Tenebrrionidae). Annals of the Entomological Society of America.(1965); 58: 535-540.
83. Tracey, K. M. Effects of parental age on the life cycle of the mealworm, *Tenebriomolitor*Linnacus. Annals of the Entomological Society of America.(1958); 51: 429-432.
84. Ludwig, D. & Fiore, C. Further studies on the relationship between parental age and the life cycle of the meal worm *Tenebriomolitor*. Annals of the Entomological Society of America. (1960); 53:595.
85. Lansing, A.I. A transmissible, cumulative and reversible factor in aging. Journal of Gerontology. (1947); 2:228-239.
86. Lansing, A.I. Evidence of aging as a consequence of growth cessation. Proc. Natl. Acad. Sci. U.S.A.(1948); 34: 304-310.
87. Lansing, A.I. A nongenetic factor in the longevity of rotifers. Annals of New York Academy of Sciences. (1954); 57: 455-464.
88. Redfield, H. Mating and the relationship of recombination to maternal age in *Drosophila melanogaster*. Genetics. (1966);53(3):593-607
89. Barbosa, P., Martinat, P. & Bennett, R. Consequences of maternal age and host deprivation on the production & development of *Brachymeriaintermedia* (Nees) and the mortality of its gypsy moth (*Lymantriadispar* L.) host. Journal of Applied Entomology. (1986); 101:215-223.
90. Priest, N. K., Mackowiak, B. and Promislow, D.E.L. The role of parental age effect on the evolution of aging. Evolution. (2002); 56(5): 927-935.
91. Singh K. & Omkar. Effect of Parental Ageing on Offspring Developmental & Survival Attributes in an Aphidophagous Ladybird, *Cheilomenessexmaculata.* Journal of Applied Entomology. (2009); 133(7): 500–504, August 2009
92. Partridge, L. and Farquhar, M. Sexual activity reduces lifespan of male fruitflies. Nature.(1981); 294:580-582.
93. Roitberg, B.D. The cost of reproduction in rosehip flies, *Rhagoletisbasiola*: eggs are time. Evolutionary Ecology. (1989); 3:183-188.
94. Tatar, M., Carey, J.R. &Vaupel, J.W. Long-term cost of reproduction with and without accelerated senescence in *Callosobruchusmaculatus*: Analysis of age- specific mortality. Evolution. (1993); 47:1302-1312.

95. Babu, A. and Anantha krishnan, T.N. Predatory efficiency, reproductive potential and bio-energetics of *Coccinella-transversalis* F. and *Meno-chilussexma-culatus* F. (Coleoptera: Coccinellidae) in relation to aphid (Homoptera: Aphididae) prey quality. Phytophaga. (1993); 5: 121-133
96. Dixon, A.F.G. Insect Predator-Prey Dynamics, Ladybird Beetles and Bio-logical Control. Cambridge University Press. (2000); pp. 257.
97. Williams, G.C. Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist. (1966); 100:687-690.
98. Gadgil, M. &Bossert, W. H. Life historical consequences of natural selection. The American Naturalist. (1970); 104:1-24.
99. Bell, G. &Koufopanou, V. The cost of reproduction. In: Oxford Surveys in Evolutionary Biology (eds. Dawkins, R. & Ridley, M.). Oxford University Press. (1985); P. 83-131.
100. Partridge, L. & Harvey, P.H. Evolutionary biology: costs of reproduction. Nature. (1985); 316:20-21.
101. Reznick, D. The cost of reproduction: an evaluation of the empirical evidence. Oikos. (1985); 44:257-267.
102. Dixon, A.F.G. and Kundu, R. Trade-off between reproduction and length of adult life in males and mating females of aphids. European Journal of Entomology. (1997); 94: 105-109.
103. Sgrò, C. and Partridge, L. A delayed wave of death from reproduction in *Drosophila*. Science. (1999); 286: 2521-2524.
104. Rose, M. Anatgonisticpleiotropy, dominance and genetic variation. Heredity. (1982); 48: 63-78