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Bibliography on female remating, sperm storage, and sperm competition in *Drosophila*.

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This bibliography includes the papers published on female remating, sperm storage, sperm competition and its consequences such as sperm precedence or sperm displacement with role of male accessory gland fluids in female remating in several species of *Drosophila*. Female remating is fundamental to evolutionary biology as it determines the pattern of sexual selection and sexual conflict. Remating in females is an important component of *Drosophila* mating systems, because females store the sperm after mating in the spermathecae and ventral receptacles and utilize them to fertilize eggs as they are laid. The phenomenon of remating by females is a prerequisite for the occurrence of sperm competition between males. The total impact of sperm competition on male fitness and significant effect of remating on the fitness of female, combine to make an excellent example of sexual selection. However, the abstracts of symposia and conferences have not been included. In this bibliography we have tried to cover the literature on female remating, sperm storage and sperm competition up to April 2002. We apologize to the readers for inadvertent omission of any paper. One (SRS) of the authors thanks the CSIR, New Delhi for the award of Senior Research Fellowship (SRF) to him.

- Akin, E., H. Levene, L. Levine and R. Rockwell. 1984. A conservative procedure for the estimation of multiple insemination in *Drosophila*. *Am. Nat.* 124: 723-737.
- Anderson, W. W. 1974. Frequent multiple insemination in a natural population of *D. pseudoobscura*. *Am. Nat.* 108: 709-711.
- Arthur, B. I., E. Hauschteck-Jungen, R. Nothiger and P. I Ward. 1998. A female nervous system is necessary for normal sperm storage in *D. melanogaster*: A masculinized nervous system is as good as none. *Proc. Roy. Soc. London Ser B* 265: 1749-1773.
- Aspi, J. 1992. Incidence and adaptive significance of multiple mating in females of two boreal *D. virilis* group species. *Ann. Zool. Fenn.* 29: 147-159.
- _____, and P. Lankinen. 1992. Frequency of multiple insemination in a natural population of *D. montana*. *Hereditas* 117: 169-177.
- Barbadilla, A., J. E. Quezada-Diaz, A. Ruiz, M. Santos and A. Fontdevila. 1991. The evolutionary history of *D. buzzatii*. XVII. Double mating and sperm predominance. *Genet. Sel. Evol.* 23: 133-140.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349-368.
- Beckenbach, A. T. 1981. Multiple mating and sex-ratio in *D. pseudoobscura*. *Evolution* 35: 275-281.
- Begun, D. J., P. Whitley, B. L. Todd, H. M. Waldrip-Dial and A. G. Clark. 2000. Molecular population genetics of accessory gland proteins in *Drosophila*. *Genetics* 156: 1879-1888.
- Bertram, M. J., D. M. Neubaum, and M. F. Wolfner. 1996. Localization of the *Drosophila* accessory gland protein Acp36DE in the mated female suggests a role in sperm storage. *Insect Bioch. Mol. Biol.* 26: 971-980.

- Birkhead, T. R. and A. P. Møller. 1998. Sperm competition and sexual selection. Academic Press, London.
- Boorman, E. and G. A. Parker. 1976. Sperm (ejaculate) competition in *D. melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecol. Entomol.* 1: 145-155.
- Bouletreau-Merle, J. 1977. Role des spermatheques dans l' utilization du sperme et la stimulation de l' ovogenese chez *D. melanogaster*. *J. Insect Physiol.* 23: 1099-1104.
- Bressac, C. A. Fleury and D. Lachaise. 1994. Another way of being anisogamous in *Drosophila* subgenus species: Giant sperm, one to one gamete ratio, and high zygote provisioning. *Proc. Natl. Acad. Sci. USA.* 91: 10399-10402.
- _____, and E. Hauschteck-Jungen. 1996. *D. subobscura* females preferentially select long sperm for storage and use. *J. Insect Physiol.* 42: 323-328.
- _____, D. Joly, J. Devaux and D. Lachaise. 1991. Can we predict the mating pattern of *Drosophila* females from the sperm length distribution in males? *Experientia* 47: 111-114.
- Bundgaard, J. and F. B. Christiansen. 1972. Dynamics polymorphism. I. Selection components in an experimental population of *D. melanogaster*. *Genetics* 71: 439-460.
- _____, J. and J. S. F. Barker. 2000. Remating, sperm transfer, and sperm displacement in cactophilic species *D. buzzatii* Patterson & Wheeler (Diptera: Drosophilidae). *Biol. J. Linn. Soc.* 71: 145-164.
- Chapman, T. 2001. Seminal fluid-mediated fitness traits in *Drosophila*. *Heredity* 87: 511-521.
- _____, and L. Partridge. 1996. Female fitness in *D. melanogaster*: an interaction between the effect of nutrition and of encounter rate with males. *Proc. Roy. Soc. London B* 263: 755-759.
- _____, D. M. Neubaum, M. T. Wolfner and L. Partridge. 2000. The role of male accessory gland protein Acp 36DE in sperm competition in *D. melanogaster*. *Proc. Royl. Soc. London Ser B.* 267: 1097-1105.
- _____, L. F. Liddle, J. M. Kalb, M. F. Wolfner and L. Partridge. 1995. Cost of mating in *D. melanogaster* females is mediated by male accessory gland products. *Nature* 373: 241-244.
- _____, S. Trevitt and L. Partridge. 1994. Remating and male derived nutrients in *D. melanogaster*. *J. Evol. Biol.* 7: 51-69.
- Chen, P. S. 1984. The functional morphology and biochemistry of male accessory gland and their secretion. *Ann. Rev. Entomol.* 29: 233-255.
- _____. 1996. The accessory gland proteins in male *Drosophila*: structural, reproductive and evolutionary aspects. *Experientia* 52: 503-510.
- _____, E. Stumm-Zollinger, T. Aigaki, J. Balmer, M. Bienz and P. Bohen. 1988. A male accessory gland peptide that regulates reproductive behavior of female *D. melanogaster*. *Cell* 54: 291-298.
- Childress, D. and D. L. Hartl. 1972. Sperm preference in *D. melanogaster*. *Genetics* 71: 417-427.
- Civetta, A. 1999. Direct visualization of sperm competition and sperm storage in *Drosophila*. *Curr. Biol.* 9: 841-844.
- _____, and A. G. Clark. 2000a. Chromosomal effects on male and female components of sperm precedence in *Drosophila*. *Genet. Res.* 75: 143-151.
- _____, and _____. 2000b. Correlated effects of sperm competition and postmating female mortality. *Proc. Natl. Acad. Sci. USA* 97: 13162-13165.
- Civetta, A. H. M. Waldrip-Dail and A. G. Clark. 2002. An introgression approach to mapping differences in mating success and sperm competitive ability in *Drosophila simulans* and *D. sechellia*. *Genet. Res.* 79: 65-74.
- Clark, A. G. 2002. Sperm competition and the maintenance of polymorphism. *Heredity* 88: 148-153.

- _____, and D. J. Begun. 1998. Female genotypes affect sperm displacement in *Drosophila*. *Genetics* 149: 1487-1493.
- _____, _____, and T. Prout. 1999. Female x male interaction in *Drosophila* sperm competition. *Science* 283: 217-220.
- _____, E. T. Dermitzakis and A. Civetta. 2000. Nontransitivity of sperm precedence in *Drosophila*. *Evolution* 54: 1030-1035.
- _____, M. Aguade, T. Prout, L. G. Harshman and C. H. Langley. 1995. Variation in sperm displacement and its association with accessory gland protein loci in *D. melanogaster*. *Genetics* 139: 189-201.
- Cobbs, G. 1977 Multiple insemination and male sexual selection in natural population of *D. pseudoobscura*. *Am. Nat.* 111: 641-656.
- Craddock, E. M. and W. E. Johnson. 1978. Multiple insemination in natural populations of *D. silvestris*. *Dros. Inf. Serv.* 53: 138-139.
- Curtsinger, J. W. 1991. Sperm competition and evolution of multiple mating. *Am. Nat.* 138: 93-102.
- De Vries, J. K. 1964. Insemination and sperm storage in *Drosophila*. *Evolution* 18: 271-282.
- Dobzhansky, Th. and O. Pavlovsky. 1967. Repeated mating and sperm mixing in *D. pseudoobscura*. *Am. Nat.* 101: 527-533.
- Ehrlich, E. 1959. The pattern of sperm utilization by multiple inseminated females. *Dros. Inf. Serv.* 33: 129-130.
- Etges, W. J. and W. B. Heed. 1992. Remating effects on the genetic structure of female life histories in populations of *D. mojavensis*. *Heredity* 68: 515-528.
- Fan, Y., A. Rafaeli, P. Moshitzky, E. Kubli, Y. Choffat and S. W. Applebaum. 2000. Common functional elements of *D. melanogaster* seminal peptides involved in reproduction of *D. melanogaster* and *H. armigera*. *Insect Bioch. Mol. Biol.* 30: 805-812.
- Fowler, G. L. 1973. Some aspects of the reproductive biology of *Drosophila*: sperm storage and sperm utilization. *Adv. Genet.* 17: 293-360.
- _____, K. E. Eroshevich and S. Zimmering. 1968. Distribution of sperm in the storage organs of the *D. melanogaster* female at various levels of insemination. *Mol Gen Genet.* 101:120-122.
- Fuerst, P. A., W. W. Pendlebury and J. F. Kidwell. 1973. Propensity for multiple mating in *D. melanogaster*. *Evolution* 27: 265-268.
- Fukui, H. H. and M. H. Gromko. 1989. Female receptivity to remating and early fecundity in *D. melanogaster*. *Evolution* 43: 1311-1315.
- _____, and _____. 1991a. Genetic basis for remating in *D. melanogaster*. IV. A chromosome substitution analysis. *Behav. Genet.* 21: 169-182.
- _____, and _____. 1991b. Genetic basis for remating in *D. melanogaster*. V. Biometrical and planned comparison analysis. *Behav. Genet.* 21: 183-197.
- _____, and _____. 1991c. Genetic basis for remating in *D. melanogaster*. VI. Recombination analysis. *Behav. Genet.* 21: 199-209.
- Fuyama, Y. 1995. Genetic evidence that ovulation reduces sexual receptivity in *D. melanogaster* females. *Behav. Genet.* 25: 581-587.
- _____, and M. Ueyama. 1997. Ovulation and the suppression of mating in *D. melanogaster* females: Behavioural basis. *Behav. Genet.* 27: 483-488.
- Gilbert, D. G. 1981a. Sperm counts and initial sperm storage in *D. melanogaster*. *Dros. Inf. Serv.* 56: 46-47.
- _____. 1981b. Ejaculate esterase 6 and initial sperm use by female *D. melanogaster*. *J. Insect Physiol.*, 27: 641-650.

- _____, and R. C. Richmond. 1981. Studies of esterase 6 in *D. melanogaster*: VI. Ejaculate competition abilities of males having null or active alleles. *Genetics* 97: 85-94.
- _____, and _____. 1982. Esterase-6 in *D. melanogaster*: Reproductive function of active and null males at low temperature. *Proc. Natl. Acad. Sci. USA* 79: 2962-2966.
- Gilchrist, A. S. and L. Partridge. 1995. Male identity and sperm displacement in *D. melanogaster*. *J. Insect Physiol.* 27: 641-650.
- _____, and _____. 1997. Heritability of pre-adult viability differences can explain apparent heritability of sperm displacement ability in *D. melanogaster*. *Proc. R. Soc. Lond. Ser B* 264: 1271-1275.
- _____, and _____. 2000. Why it is difficult to model sperm displacement in *D. melanogaster*: The relation between sperm transfer and copulation duration. *Evolution* 54: 534-542.
- Griffiths, R. C., S. W. McKechnie and J. A. McKenzie. 1982. Multiple mating and sperm displacement in a natural population of *D. melanogaster*. *Theor. Appl. Genet.* 62: 89-96.
- Gromko, M. H. 1992. Genetic correlation of male and female mating frequency: Evidence from *D. melanogaster*. *Anim. Behav.* 43: 176-177.
- _____, and D. W. Pyle. 1978. Sperm competition, male fitness, and repeated mating by female *D. melanogaster*. *Evolution* 32: 588-593.
- _____, and M. E. A. Newport. 1988a. Genetic basis for remating in *D. melanogaster*. II. Response to selection based on the behaviour of one sex. *Behav. Genet.* 18: 621-632.
- _____, and _____. 1988b. Genetic basis for remating in *D. melanogaster*. II. Correlated responses to selection for female remating speed. *Behav. Genet.* 18: 633-643.
- _____, and P. D. Gerhart. 1984. Increased density does not increase remating frequency in laboratory populations of *D. melanogaster*. *Evolution* 38: 451-455.
- _____, and T. A. Markow. 1993. Courtship and remating in field populations of *Drosophila*. *Anim. Behav.* 45: 253-262.
- _____, D. G. Gilbert and R. C. Richmond. 1984. Sperm transfer and use in the multiple mating system of *Drosophila*. In: *Sperm Competition and the Evolution of Animal Mating Systems* pp. 372-427, (Smith, R. L., ed.), Academic Press, New York.
- _____, K. Sheehan and _____. 1980. Random mating in two species of *Drosophila*. *Am. Nat.* 115: 467-479.
- _____, M. E. A. Newport and M. G. Kortier. 1984. Sperm dependence of female receptivity to remating in *D. melanogaster*. *Evolution* 38: 1273-1282.
- Haig, D. and C. T. Bergstrom. 1995. Multiple mating, sperm competition and meiotic drive. *J. Evol. Biol.* 8: 265-282.
- Harshman, L. G. and A. A. Hoffmann. 1987. Experimental design and remating in *D. melanogaster*. 66: 74.
- _____, and A. G. Clark. 1998. Interference of sperm competition from broods of field-caught *Drosophila*. *Evolution* 52: 1334-1341.
- _____, and T. Prout. 1994. Sperm displacement without sperm transfer in *D. melanogaster*. *Evolution* 48: 758-766.
- _____, A. A. Hoffmann and T. Prout. 1988. Environmental effects on remating in *D. melanogaster*. *Evolution* 42: 312-321.
- Heifetz, Y., O. Lung, E. E. A. Frongillo Jr, and M. F. Wolfner. 2000. The *Drosophila* seminal fluid protein Acp 26 Aa stimulates release of oocytes by the ovary. *Curr. Biol.* 10: 99-102.
- _____, U. Tram and M. F. Wofner. 2001. Male contributions to egg production: the role of accessory gland products and sperm in *D. melanogaster*. *Proc. R. Soc. Lond. B* 268: 175-180.

- Herdon, L. A. and M. F. Wolfner. 1995. A *Drosophila* seminal fluid, Acp26Aa, stimulates egg laying in females for one day following mating. *Proc. Natl. Acad. Sci. USA* 92: 1014-1018.
- Hihara, F. 1981. Effects of the male accessory gland secretion on oviposition and remating in females of *D. melanogaster*. *Zool. Mag.* 90: 303-316.
- Hirai, Y. and M. T. Kimura. 1999. Effects of copulation duration on fertility and sexual receptivity of females of *D. elegans*. *Zool. Sci.* 16: 417-421.
- Holland, B. and W. R. Rice. 1999. Experimental removal of sexual selection reverses inter-sexual antagonistic co-evolution and removes reproductive load. *Proc. Natl. Acad. Sci. USA* 96: 5083-5088.
- Hosken, D. J., T. W. Graner and P. I. Ward. 2001. Sexual conflict selects for male and female reproductive characters. *Curr Biol.* 11: 489-493.
- Howard, D., P. G. Gregory, J. Chu and M. L. Cain. 1998. Conspecific sperm precedence is an effective barrier to hybridization between closely related species. *Evolution* 52: 511-516.
- Hughes, K. A. 1997. Quantitative genetics of sperm precedence in *D. melanogaster*. *Genetics* 145: 139-151.
- Hunter, F. M. and T. R. Birkhead. 2002. Sperm viability and sperm competition in insects. *Curr. Biol.* 12:121-123.
- Ikeda, H. 1974. Multiple copulation: An abnormal mating behavior, which deleteriously affects fitness in *D. mercatorum*. *Mem. Ehime. Univ. Sci. Ser. B* 3: 18-28.
- Iliadi, K., N. Iliadi, E. Raskovetsky, I. Minkow, E. Nevo and A. Korol. 2001. Sexual and reproductive behavior of *Drosophila melanogaster* from a microclimatically interslope differentiated population of 'Evolution canyon' (mount carmel, Israel). *Proc. R. Soc. Lond. B* 268: 2365-2374.
- Imhoff, M., B. Harr, G. Brem and C. Schlotterer. 1998. Multiple mating in wild *D. melanogaster* revisited by microsatellite analysis. *Mol. Ecol.* 7: 915-917.
- Johnsen, R. C. and S. Zarrow. 1971. Sperm competition in the *Drosophila* female. *Mol. Gen. Genet.* 110: 36-39.
- Johnson, N. 2002. Why is seminal fluid toxic? *Trends Genet.* 18: 181.
- Joly, D. and D. Lachaise. 1993. Multiple mating frequency differs in two different geographic strains of *D. teissieri*. *Dros. Inf. Serv.* 72: 126-127.
- _____, C. Bressac and D. Lachaise. 1995. Disentangling giant sperm. *Nature* 377: 202.
- _____, M. L. Cariou and D. Lachaise. 1991. Can sperm competition explain sperm polymorphism in *D. teissieri*? *Evol. Biol.* 5: 25-44.
- Karr, T. L. and S. Pitnick. 1996. The ins and outs of fertilization. *Nature* 379: 405-406.
- _____, and _____. 1999. Sperm competition: defining the rules of engagement. *Curr. Bio.* 9: R787-R790.
- Kaufman, B. P. and M. Demerec. 1942. Utilization of sperm by the female *D. melanogaster*. *Am. Nat.* 76: 445-469.
- Knowles, L. L. and T. A. Markow. 2001. Sexually antagonistic co-evolution of a postmating-prezygotic reproductive character in desert *Drosophila*. *Proc. Nat. Acad. Sci.* 98: 8692-8696.
- Koref-Santibanez, S. 2001. Effects of age and experience on mating activity in the sibling species of *D. pavani* and *D. gaucha*. *Behav. Genet.* 31: 287-297.
- Kubli, E. 1992. The sex peptide. *Bioessays.* 14: 779-784.
- _____. 1996. The *Drosophila* sex-peptide: A peptide pheromone involved in reproduction. *Adv. Dev. Biochem.*, 4: 99-128.

- Lachaise, D. and D. Joly. 1991. Sperm and evolution: Morphological and molecular aspects. In: Molecular Techniques in taxonomy, pp. 201-216, G. M. Hewitt et al. (eds.). Springer Verlag, Berlin.
- _____, Bressac, C. and D. Joly. 1991. Polymorphism, competition and evolution of spermatozoides. Pathol. Biol. 39: 654-657.
- Lefevre, G. and U. B. Jonsson. 1962a. Sperm relationship in twice-mated *D. melanogaster* females. Dros. Inf. Serv. 36: 85-86.
- _____, and _____. 1962b. Sperm transfer, storage, displacement and utilization in *D. melanogaster*. Genetics 47: 1719-1736.
- Letsinger, J. T. and M. H. Gromko. 1985. The role of sperm numbers in sperm competition and female remating in *D. melanogaster*. Genetics 66: 195-202.
- Levine, L., M. Asmussen, O. Olvera, J. R. Powell, M. E. Delarosa, V. M. Salceda, M. I. Gaso, J. Gujman and W. W. Anderson. 1980. Population genetics of Mexican *Drosophila*. V. A high rate of multiple insemination in a natural population of *D. pseudoobscura*. Am. Nat. 116: 493-503.
- _____, O. Olvera, M. I. Gaso, R. F. Rockwell, F. Gonzalez, M. E. Dela rosa and J. Gujman. 1987. Chromosomal and behavioral studies of Mexican *Drosophila*: Frequencies of multiple insemination in three natural populations. Am. Nat. 129: 458-462.
- Lobashov, M. E. 1939. Mixture of sperm in case of polyandry in *D. melanogaster*. Com. Rend (Doklady) Acad. Sci. USSR. 23: 827-830.
- Loukas, M., Y. Vergini and C. B. Krimbas. 1981. The genetics of *D. subobscura* populations. XVII. Multiple insemination and sperm displacement in *D. subobscura*. Genetica 57: 29-37.
- Lung, O. and M. F. Wolfner. 2001. Identification and characterization of the major *D. melanogaster* mating plug protein. Insect Biochem. Mol. Biol. 31: 543-551.
- _____, U. Tram, C. M. Finnerty, M. A. Eipper-Mains, J. M. Kalb and M. F. Wolfner. 2002. The *D. melanogaster* seminal fluid protein Acp62F is a protease inhibitor that is toxic upon ectopic expression. Genetics 160: 211-224.
- Manning, A. 1962. A sperm factor affecting the receptivity of *D. melanogaster* females. Nature 194: 252-253.
- _____. 1967. The control of sexual receptivity in female *Drosophila*. Anim. Behav. 15: 239-250.
- Markow, T. A. 1982. Mating systems of cactophilic *Drosophila*. In: Ecological genetics and Evolution: The cactus-yeast-*Drosophila* model system, pp. 273-287, (J. R. F. Barker and W. T. Starmer, eds.), Academic Press, Australia.
- _____. 1985. A comparative investigations of mating system of *D. hydei*. Anim. Behav. 33: 775-781.
- _____. 1996. Evolution of *Drosophila* mating systems. In: Evolutionary Biology, vol. 29, pp. 73-106, M. K. Hecht (ed.), Plenum press, New York.
- _____. 1997. Assortative fertilization in *Drosophila*. Proc. Natl. Acad. Sci. USA, 94: 7756-7760.
- _____. 2000. Forced matings in natural populations of *Drosophila*. Amer. Nat. 156: 100-103.
- _____, and P. F. Ankey. 1984. *Drosophila* males contribute to oogenesis in a multiple mating species. Science 224: 302-303.
- _____, D. Bustoz and S. Pitnick. 1996. Sexual selection and secondary sexual character in *Drosophila*. Anim. Behav. 52: 759-766.
- _____, P. D. Gallagher and R. A. Krebs. 1990. Ejaculate-derived nutritional contribution and female reproductive success in *D. mojavensis* (Patterson and Low). Funct. Ecol. 4: 67-73.
- Marks, R. W., R. D. Seager, F. J. Ayala and L. G. Barr. 1988. Local ecology and multiple matings in a natural population of *D. melanogaster*. Am. Nat. 131: 918-923.

- Maynard-Smith, J. 1956. Fertility, mating behaviour and sexual selection in *D. subobscura*. *J. Genet.* 54: 261-279.
- McRobert, S. P., C. R. Adams, M. Wutjke, J. Frank and L.L. Jackson. 1997. A comparison of female post-copulatory behaviour in *D. melanogaster* and *D. biarmipes*. *J. Insect Behav.* 10: 761-770.
- Mery, F. and D. Joly. 2002. Multiple mating, sperm transfer and oviposition pattern in the giant species, *D. bifurca*. *J. Evol. Biol.* 15: 49-56.
- Meyr, H. U., and E. R. Meyer. 1961. Sperm utilization from successive copulations in females of *D. melanogaster*. *Dros. Inf. Serv.* 35: 90-92.
- Milkman, R. and R. R. Zeitler, R. R. (1974). Concurrent multiple paternity in natural populations of *D. melanogaster*. *Genetics* 78: 1191-1193.
- Minamori, S. and K. Fukui. 1970. Sperm displacement induced by remating in female reproductive organs of *D. melanogaster*. *J. Hiroshima Univ. Ser B, Div. 1*, 23: 17-27.
- Neubaum, D. M. and M. F. Wolfner. 1999a. Mated *D. melanogaster* females require a seminal fluid protein, Acp 36PE to store sperm efficiently. *Genetics* 153: 845-857.
- _____, and _____. 1999b. Wise, winsome, or wierd? Mechanisms of sperm storage in female animals. *Curr. Topics Dev. Biol.* 41: 67-97.
- Newport, M. E. A. and M. H. Gromko. 1984. The effect of experimental design on female receptivity to remating and its impact on reproductive success in *D. melanogaster*. *Evolution* 38: 1261-1272.
- Nonidez, J. F. (1920). The internal phenomenon of reproduction in *Drosophila*. *Biol. Bull.*, 39: 1261-1272.
- Ochando, M. D., A. Reyes and F. J. Ayala. 1996. Multiple paternity in two natural populations (Orchard and Vinayard) of *Drosophila*. *Proc. Natl. Acad. Sci. USA* 93: 11769-11773.
- Ohashi, Y., K. Hamo-Fukushima and Y. Fuyama. 1991. Purification and characterization of an ovulation stimulating substance from the male accessory glands of *D. suzukii*. *Insect Biochem.* 21: 413-419.
- Olivieri, G., G. Avallone and L. Pica. 1970. Sperm competition and sperm loss in *D. melanogaster* females fertilized by $Y^S X$. Y^L/O males. *Genetics* 64: 323-335.
- Park, M. and M. F. Wolfner. 1995. Male and female cooperate in the processing of a *D. melanogaster* seminal fluid protein. *Dev. Biol.*, 171: 694-702.
- Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45: 525-567.
- Partridge, L. and L. D. Hurst. 1998. Sex and conflict. *Science* 281: 2003-2008.
- _____, and M. Farquhar. 1981. Sexual activity reduces lifespan of male fruitflies. *Nature* 294: 580-582.
- Petit, C., P. Bourgeron and H. Mercot. 1980. Multiple matings, effective population size and sexual selection in *D. melanogaster*. *Heredity* 45: 281-292.
- Pitnick, S. 1991. Male size influences mate fecundity and remating interval in *D. melanogaster*. *Anim. Behav.* 41: 735-745.
- _____. 1993. Operational sex ratios and sperm limitation in populations of *D. pachea*. *Behav. Ecol. Sociobiol.* 33: 383-391.
- _____. 1996. Investment in testes and the cost of making long sperm in *Drosophila*. *Am. Nat.* 148: 57-80.
- _____, and G. T. Miller. 2000. Correlated response in reproductive and life history traits to selection on testis length in *D. hydei*. *Heredity* 84: 416-426.

- _____, and T. A. Markow. 1994a. Male gametic strategies: Sperm size, testes size and the allocation of ejaculate among successive mates by the sperm-limited fly *D. pachea* and its relatives. *Am. Nat.* 143: 785-819.
- _____, and _____. 1994b. Large-male advantages associated with costs of sperm production in *D. hydei*, a species with giant sperm. *Proc. Natl. Acad. Sci. USA.* 91: 9277-9281.
- _____, G. S. Spicer and T. A. Markow. 1995. How long is a giant sperm? *Nature* 375: 109.
- _____, _____, and _____. 1997. Phylogenetic examination of female incorporation of ejaculate in *Drosophila*. *Evolution* 51: 833-845.
- _____, G. T. Miller, J. Reagan, and B. Holland. 2001. Males' evolutionary responses to experimental removal of sexual selection. *Proc. Roy. Soc. London, Ser. B* 268: 1071-1080.
- _____, T. A. Markow and G. S. Spicer. 1995. Delayed male maturity is a cost of producing large sperm in *Drosophila*. *Proc. Natl. Acad. Sci. USA* 92: 10614-10618.
- _____, _____, and _____. 1999. Evolution of multiple kinds of female sperm-storage organs in *Drosophila*. *Evolution* 53: 1804-1822.
- _____, _____, and M. F. Riedly. 1991. Transfer of ejaculate and incorporation of male-derived substances by females in the *nannoptera* species group (Diptera: Drosophilidae). *Evolution* 45:774-780.
- _____, W. D. Brown, and G. T. Miller. 2001. Evolution of female remating behaviour following experimental removal of sexual selection. *Proc. Roy. Soc. Lond. Ser B* 268:557-563.
- Polak, M., L. L. Wolf, W. T. Starmer and J. S. F. Barker. 2001. Function of the mating plug in *D. hibisci* Bock. *Behav. Ecol. Sociobiol.* 49: 196-205.
- Price, C. S. C. 1997. Conspecific sperm precedence in *Drosophila*. *Nature* 388: 663-666.
- _____, C. H. Kim, J. Posluszny and J. A. Coyne. 2000. Mechanisms of con-specific sperm precedence in *Drosophila*. *Evolution* 54: 2028-2037.
- _____, Dyer, K. A. and J. A. Coyne. 1999. Sperm competition between *Drosophila* males involves both displacement and incapacitation. *Nature* 400: 449-452.
- _____, H. Kim, C. J. Gronlund and J. A. Coyne. 2001. Cryptic reproductive isolation in the *D. simulans* species complex. *Evolution* 55: 81-92.
- Prout, T. and A. G. Clark. 1996. Polymorphism in genes that influence sperm displacement. *Genetics* 144: 401-408.
- _____, and _____. 2000. Seminal fluid causes temporarily reduced egg hatch in previously mated females. *Proc. Roy. Soc. London. Ser B.* 267: 201-203.
- _____, and J. Bundgaard. 1977. The population genetics of sperm displacement. *Genetics* 85: 95-124.
- Pruzan Hotchkiss, A., D. Dejjane and S. H. Faro. 1981. Sperm utilization in once and twice mated *D. pseudoobscura* female. *Am. Nat.* 118: 37-45.
- Pruzan, A. 1976. Effects of age, rearing and mating experiences on frequency dependent sexual selection in *D. pseudoobscura*. *Evolution* 30: 130-145.
- Pulvermacher, C. and K. Timmer. 1977. Influence of double matings on the offspring of *D. melanogaster*. *Dros. Inf. Serv.* 52: 149-150.
- Pyle, D. W. and M. H. Gromko. 1978. Repeated mating by female *D. melanogaster*: The adaptive importance. *Experientia* 34: 449-450.
- _____, and _____. 1981. Genetic basis for repeated mating in *D. melanogaster*. *Am. Nat.* 117: 133-146.
- Rice, R. 1996. Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* 381: 232-234.

- Richmond, R. C. 1976. Frequency of multiple insemination in natural populations of *Drosophila*. *Am. Nat.* 110: 485-486.
- _____, and A. Senior 1981. Esterase -6 of *D. melanogaster*: Kinetics of transfer to females, decay in females and male recovery. *J. Insect Physiol.* 27: 849-853.
- _____, and J. R. Powell 1970. Evidence of heterosis associated with an enzyme locus in a natural population of *Drosophila*. *Proc. Natl. Acad. Sci. USA* 67: 1264-1267.
- _____, and L. Ehrman. 1974. The incidence of repeated mating in the superspecies *D. paulistorum*. *Experientia* 30: 489-490.
- Ridley, M. 1988. Mating frequency and fecundity in insects. *Biol. Rev.* 63: 509-549.
- _____. 1989. The incidence of sperm displacement in insects: Four conjectures, one corroboration. *Biol. J. Linn. Soc.* 38: 349-367.
- Ringo, J. 1996. Sexual receptivity in insects. *Ann. Rev. Entomol.* 41: 473-494.
- Russell, J. S., B. L. Ward and W. B. Heed. 1977. Sperm storage and hybridization in *D. nanoptera* and related species. *Dros. Inf. Serv.* 52: 70.
- Schwartz, J. M. and C. R. B. Boake. 1992. Sexual dimorphism in remating in Hawaiian *Drosophila* species. *Anim. Behav.* 44: 231-238.
- Scott, D. 1986. Inhibition of female *D. melanogaster* remating by a seminal fluid protein (esterase 6). *Evolution* 40: 1084-1091.
- _____. 1987. The timing of the sperm effect on female *D. melanogaster* receptivity. *Anim. Behav.* 35: 142-149.
- _____, and E. Williams. 1993. Sperm displacement after remating in *D. melanogaster*. *J. Insect Physiol.* 39: 201-206.
- _____, and R. C. Richmond. 1990. Sperm loss by remating in *D. melanogaster* females. *J. Insect Physiol.* 39: 201-206.
- Service, P. M. and A. J. Fales. 1993. Evolution of delayed reproductive senescence in male fruit flies: Sperm competition. *Genetica* 91 111-125.
- _____, and R. E. Vossbrink. 1996. Genetic variation in "First" male effect on egg laying and remating by female *D. melanogaster*. *Behav. Genet.* 26: 39-48.
- Sgro, C. M. and L. Partridge. 1999. A delayed wave of death from reproduction in *Drosophila*. *Science* 286: 2521-2524.
- _____, and _____. 2000. Evolutionary responses of the life history of wild-caught *D. melanogaster* to two standard methods of laboratory culture. *Am. Nat.* 156: 341-353.
- _____, G. Geddes, K. Fowler, and L. Partridge. 2000. Selection on age at reproduction in *D. melanogaster*: Female mating frequency as a correlated response. *Evolution* 54: 2152-2155.
- _____, T. Chapman and L. Partridge. 1998. Sex-specific selection on time to remate in *D. melanogaster*. *Anim. Behav.* 56: 1267-1278.149.
- Sharp, P. M. 1982. Competitive mating in *D. melanogaster*. *Genet. Res.* 40: 201-205.
- Singh, B.N. and S. R. Singh. 1999. Female remating in *D. ananassae*: Shorter duration of copulation during second mating as compared to first mating. *J. Biosci.* 24: 427-431.
- _____, and _____. 2001. Female remating in *D. ananassae*: Evidence for sperm displacement and greater productivity after remating. *Zool. Sci.* 18: 181-185.
- Singh, S.R. and B.N. Singh. 1997. Female remating in *D. ananassae*. *Dros. Inf. Ser.* 80: 38-39.
- _____, and _____. 2001a. Female remating in *D. ananassae*: Evidence for the effect of density on female remating frequency. *J. Insect Behav.* 14: 659-668.
- _____, and _____. 2001b. Female remating in *D. ananassae*: Bidirectional selection for remating speed. *Behav. Genet.* 31: 361-370.

- _____, _____, and H. F. Hoenigsberg. 2002. Female remating, sperm competition and sexual selection in *Drosophila*. Genet. Mol. Res.
- Smith, R. L. 1984. Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, New York.
- Snook, R. 1998. The risk of sperm competition and the evolution of sperm heteromorphism. Anim. Behav. 56: 1497-1507.
- _____, and T. A. Markow. 1996. Possible role of non-fertilizing sperm as a nutrient source for female *D. pseudoobscura* (Diptera: Drosophilidae). Pan. Entomol. 72: 121-129.
- _____, and _____. 2001. Mating system evolution in sperm-heteromorphic *Drosophila*. J. Insect Physiol. 47: 957-964.
- _____, and _____. 2002. Efficiency of gamete usage in nature: Sperm storage, fertilization and polyspermy. Proc. Roy. Soc. Lond. Ser B. 269: 467-473.
- _____, and T. L. Karr. 1998. Only long sperm are fertilization competent in six sperm heteromorphic *Drosophila* species. Curr Biol. 8: 291-294.
- _____, and Y. K. So. 2000. Associations between female remating behaviour, oogenesis and oviposition in *D. melanogaster* and *D. pseudoobscura*. J. Insect Physiol. 46: 1489-1149.
- _____, T. A. Markow and T. L. Karr. 1994. Functional nonequivalence of sperm in *D. pseudoobscura*. Proc. Natl. Acad. Sci. USA. 91: 11222-11226.
- Spieth, H. T. and Ringo, J. M. 1983. Mating behaviour and sexual isolation in *Drosophila*. In: The Genetics and Biology of *Drosophila*., M. Ashburner, H. L. Carson, and J. N. Thompson Jr. (eds.) Academic Press, New York, Vol 3c, pp. 223-284.
- Stalker, H. D. 1976. Enzymes and reproduction in natural populations of *D. euronotus*. Genetics 84: 375-384.
- Stone, W. S. and J. T. Patterson. 1954. III. Fertilizations in multiple matings between species of the *virilis* group. Univ. Texas Publ. 5422: 38-45.
- Svobdova, M., J. Poruba and J. K. Benedik. 1977. Frequency of multiple mating in two laboratory strains of *D. melanogaster*. Dros. Inf. Serv. 52: 30.
- Tram, U. and M. F. Wolfner. 1998. Seminal fluid regulation of female sexual attractiveness in *D. melanogaster*. Proc. Nat. Acad. Sci. USA 95: 4051-4054.
- _____, and _____. 1999. Male seminal fluid proteins are essential for sperm storage in *D. melanogaster*. Genetics 153: 837-844.
- Trevitt, S., K. Fowler and L. Partridge. 1988. An effect of egg deposition on the subsequent fertility and remating frequency of female *D. melanogaster*. J. Insect Physiol. 34: 821-828.
- Turner, M. E. 1986. Multiple mating, sperm competition and the fertility component of fitness in *D. pseudoobscura*. Florida Entomol. 69: 121-128.
- _____, and W. W. Anderson. 1983. Multiple mating and female fitness in *D. pseudoobscura*. Evolution 37: 714-723.
- _____, and _____. 1984. Sperm predominance among *D. pseudoobscura* karyotypes. Evolution 38: 983-995.
- van-Vianen, A. and R. Bijlsma. 1991. The effect of male mating status on remating of females mated to these males in *D. melanogaster*. Dros. Inf. Serv. 70: 226-227.
- _____, and _____. 1993. The adult component of selection in *D. melanogaster*. Some aspect of early remating activity in females. Heredity 71: 269-276.
- Willams, C. J. and S. Evarts. 1989. The estimation of concurrent multiple paternity probabilities in natural populations. Theor. Popl. Biol. 35: 90-112.

- Wolfner, M. F. 1997. Tokens of love: Functions and regulation of *Drosophila* male accessory gland products. *Insect Biochem. Mol. Biol.* 27: 179-192.
- _____. 2002. The gifts that keep on giving: physiological functions and evolutionary dynamics of male seminal proteins in *Drosophila*. *Heredity* 88: 85-93.
- Wu, C.-I. 1983a. Virility deficiency and the sex-ratio trait in *D. pseudoobscura*. I. Sperm displacement and sexual selection. *Genetics* 105: 651-662.
- _____. 1983b. Virility deficiency and the sex-ratio trait in *D. pseudoobscura*. II. Multiple mating and overall virility selection. *Genetics* 105: 663-679.
- Xue, L. and M. Noll. 2000. *Drosophila* female sexual behavior induced by sterile males showing copulation complementation. *Proc. Natl. Acad. Sci. USA*. 97: 3272-3275.
- Zimmering, S. and G. L. Fowler. 1968. Progeny: Sperm ratios and non-functional sperm in *D. melanogaster*. *Genet. Res.* 12: 359-363.