



Drosophila Males Contribute to Oogenesis in a Multiple Mating Species

Author(s): Therese A. Markow and Paul F. Ankney

Source: *Science*, New Series, Vol. 224, No. 4646 (Apr. 20, 1984), pp. 302-303

Published by: American Association for the Advancement of Science

Stable URL: <http://www.jstor.org/stable/1692140>

Accessed: 10/08/2009 17:33

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=aaas>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



American Association for the Advancement of Science is collaborating with JSTOR to digitize, preserve and extend access to *Science*.

<http://www.jstor.org>

tion of segregation ice and frozen sediments may represent annual temperature cycles, although this type of stratification can also occur under constant temperature conditions.

Because formation of segregation ice involves drawing additional water into the system, and because segregation ice can continue to form even under great pressure, ice island heights of 7 m are not unexpected. At most lakes, the islands probably were even higher in the past and definitely were larger in area. These ice deposits are now disappearing, and the most spectacular ones, such as those at Laguna Colorada, will probably not persist for more than a decade or two. However, their future will be strongly influenced by even small changes in lake water level, air temperature, or geothermal activity.

STUART H. HURLBERT

Department of Biology,
San Diego State University,
San Diego, California 92182

CECILY C. Y. CHANG

Water Resources Division,
U.S. Geological Survey,
Menlo Park, California 94025

References and Notes

1. G. E. Stoertz and G. E. Ericksen, *U.S. Geol. Surv. Prof. Pap.* 811 (1974).
2. O. Ballivian and F. Risacher, *Los Salares del Altiplano Boliviano* (Office de Recherche Scientifique et Technique Outre-Mer, Paris, 1981).
3. T. Vila, *Rev. Geol. Chile* 2, 41 (1975).
4. F. Ahfeld, *Geologia de Bolivia* (Los Amigos del Libro, La Paz, 1972).
5. M. Servant and J. C. Fontes, *Cah. ORSTOM Ser. Geol.* 10, 9 (1978).
6. Salinity of melted ice samples from this and other lakes ranges from less than 1 to 3 per mil, with few exceptions. Determinations made with an American Optical hand refractometer (model 10419).
7. F. C. Walcott, *Geogr. Rev.* 15, 346 (1925).
8. J. H. Mercer and O. Palacios M., *Geology* 5, 600 (1977); S. Hastenrath, *The Glaciation of the Ecuadorian Andes* (Balkema, Rotterdam, 1981); G. H. Denton and W. Karlen, *Quat. Res. (N.Y.)* 3, 155 (1973); H. H. Lamb, *Palaeogeogr. Palaeoclim. Palaeoecol.* 1, 13 (1965).
9. S. Taber, *J. Geol.* 38, 303 (1930); J. R. Mackay, *Can. J. Earth Sci.* 10, 979 (1973); *Geogr. Bull.* 8, 59 (1966); in *Proceedings of the 2nd International Conference on Permafrost* (National Academy of Sciences, Washington, D.C., 1973), p. 223; A. L. Washburn, *Geocryology* (Wiley, New York, 1980).
10. At four widely separated points in this lake, the salinity of lake water ranged from 146 to 292 per mil; salinity of pore water from 0.5 m beneath the lake bottom ranged from 5 to 15 per mil.
11. S. Hurlbert and C. Chang, *Proc. Natl. Acad. Sci. U.S.A.* 80, 4766 (1983).
12. We thank G. Bejarano and the Ministry of Agriculture of Bolivia and numerous civilian and military authorities in both Bolivia and Chile for facilitating our work. For assistance and companionship in the field we thank especially E. Berna, J. Berna, J. Berna, A. Gonzalez, J. Keith, M. Lopez, C. Mitchell, H. Marcos, L. Peña, T. Saire, and A. Vargas. Alejandro Barrero and personnel of Mina Laguna Verde provided invaluable logistical support. R. Berry, R. Lowe, S. Sitko, A. Sturz, and J. Verfaillie analyzed sediment and water samples. This paper is dedicated to Sr. Alejandro Barrero Delgado, pioneer explorer of the Sud Lipez. Supported by grants from the National Geographic Society.

20 January 1984; accepted 22 February 1984

Drosophila Males Contribute to Oogenesis in a Multiple Mating Species

Abstract. Two species of *Drosophila* that differ in their ecology and mating systems have been compared with respect to male contribution to the somatic tissues and developing oocytes of females. In the species *Drosophila mojavensis* females remate daily, exhibit a copulatory plug, and have been shown to obtain a contribution from the male ejaculate. In contrast, *Drosophila melanogaster* males do not contribute to females. Female *Drosophila melanogaster* do not remate as frequently as *Drosophila mojavensis* females nor is a copulatory plug formed.

Species of *Drosophila* show wide variability in mating systems (1). One of the most striking differences observed is the frequency at which females of various species remate. For example, mated females of the cosmopolitan species *D. melanogaster*, when provided with males every morning, usually will not remate for about 5 to 7 days (2). Under similar conditions, females of the Sonoran Desert endemic cactiphilic species *D. mojavensis* remate daily. The pattern of daily remating in *D. mojavensis* is observed even when mated females do not oviposit and even though the ventral receptacle may contain numerous sperm (1). Another difference between these two species is the formation of a reaction mass or copulatory plug following mating in *D. mojavensis* but not in *D. melanogaster* (3). The evolutionary significance of this difference in remating frequency is postulated to be linked to an interspecific difference in parental investment by males (1); specifically, *D. mojavensis* females, living in a harsh environment often with limited resources, are predicted to remate more frequently in order to obtain nutrients from the male ejaculate. We now present evidence that, during copulation, males of *D. mojavensis* con-

tribute nutrients to oocytes and to female somatic tissues while *D. melanogaster* males apparently do not.

Males were isotopically labeled by placing freshly oviposited eggs on Carolina instant *Drosophila* medium containing ³H-labeled amino acids (4). Virgin males were separated upon eclosion and stored at 24° ± 1°C until they were required for mating experiments. After 4 days, labeled *D. melanogaster* males were mated to unlabeled females. Whole *D. melanogaster* males showed an average of 28,509 disintegrations per minute at the time of mating. Labeled *D. mojavensis* males were stored for 8 days before being mated to unlabeled females; these males showed an average of about 350,000 disintegrations per minute. The developmental time of *D. mojavensis* is 50 percent longer than *D. melanogaster*, which most likely accounts for the larger size of *D. mojavensis* and their higher concentration of radioactivity. The presence of isotope in mated females was determined immediately after copulation and again 24 hours later (5). The body parts analyzed are shown in Table 1.

In both species a large amount of radioactivity was seen in the female reproductive tract (uterus, ventral recepta-

Table 1. Radioactivity found in females at two times after mating. Data presented are averages for single females. At least three replications of three females per replication were performed for each time point. Counts per minute were converted to disintegrations per minute according to a standard quench curve. Controls consisted of body parts from unlabeled females. The results are given as means ± standard errors.

Part	Radioactivity (disintegrations per minute)		
	0 hours	24 hours	t*
<i>Drosophila melanogaster</i>			
Head	18.9 ± 0.8	23.8 ± 6.1	1.39
Thorax	23.7 ± 4.6	31.1 ± 8.7	1.31
Abdomen†	39.5 ± 12.2	25.1 ± 3.1	1.09
Reproductive tract	1112.4 ± 63.1‡	50.4 ± 23.9	6.47§
Ovarian eggs	25.9 ± 9.8	23.9 ± 5.4	0.32
<i>Drosophila mojavensis</i>			
Head	31.6 ± 6.6	56.23 ± 3.6‡	5.21
Thorax	50.4 ± 8.6	98.0 ± 5.5‡	7.77§
Abdomen	28.9 ± 6.4	72.2 ± 5.3‡	10.24§
Reproductive tract	1426.7 ± 118.6‡	67.4 ± 9.1‡	84.44§
Ovarian eggs	32.2 ± 8.5	191.7 ± 20.4‡	8.622§

*When appropriate, the Welch method was used (11); otherwise two-tailed t-tests were used to compare sample means. †Minus reproductive tracts. ‡Differs significantly from unlabeled controls. §P < 0.01. ||P < 0.05.

cle, and spermathecae) immediately after copulation. At this point the amount of isotope in other parts did not differ significantly from that in control. Twenty-four hours later a large amount of isotope still remained in the reproductive tracts, although the level was reduced. In *D. melanogaster* females radioactivity decreased in the reproductive tract, and no significant amounts of isotope were detected in any other tissues after 24 hours. *Drosophila* females have been observed to expel material from their reproductive tract after mating (6), and we have assumed that this accounts for the reduction in the amount of isotope after 24 hours.

However, *D. mojavensis* females showed significant radioactivity in other body parts, especially unfertilized ovarian oocytes. Since oogenesis requires approximately the same length of time in both these species, and the same female reproductive state existed in both experiments, differential rates of oogenesis cannot be the underlying cause of the presence of isotope in *D. mojavensis* oocytes. The amount of isotope also increases in the somatic tissues of *D. mojavensis* females within 24 hours. The molecular nature of the substances transferred is still unknown, but since male contribution has also been documented with ¹⁴C-labeled amino acids (7) any major role of tritium exchange in the observation of male contribution in *D. mojavensis* can be ruled out.

After two or three consecutive matings, *D. melanogaster* males are temporarily sterile (2, 8). This sterility is caused by a reduction in male accessory gland secretions, not by a reduction in sperm number. After 24 hours, abstinent males regain their fertility (2). In contrast, *D. mojavensis* males may mate seven or more times consecutively without any observable reduction in fertility (1). It is possible that *D. mojavensis* males transfer less material at each copulation in order to take advantage of the increased mating opportunities in their population.

The phenomenon of males transferring nutrients to females which then appear in female somatic tissues and oocytes has been demonstrated in several species of Lepidoptera (7). In these two *Drosophila* species, which differ in their ecology and mating systems, a difference in male contribution to egg production is also apparent. *Drosophila melanogaster*, a cosmopolitan species, can use a variety of substrates for breeding. However, *D. mojavensis* uses necrotic tissue of organ pipe cactus in Sonora, Mexico and

southern Arizona, and agria cactus in Baja California. At certain times of the year these resources are limited, and even during times of abundant resources females are selective about the stage and condition of the necrotic tissue on which they will oviposit (9). Females must be able to manufacture eggs and also survive until finding an appropriate place to oviposit, and male nutrient contribution may help them do this. The discovery of male nutrient contribution in a genus whose phylogenetic relationships are well defined, whose mating systems vary, and whose ecology is under intensive study (10) provides a new opportunity to inquire into the evolution of mating strategies in insects.

THERESE A. MARKOW

PAUL F. ANKNEY

Department of Zoology,
Arizona State University,
Tempe 85287

References and Notes

1. T. A. Markow, in *Ecological Genetics and Evolution: The Cactus-Yeast-Drosophila Model System*, J. S. F. Barker and W. T. Starmer, Eds. (Academic Press, Sydney, 1982); *Anim. Behav.*, in press.
2. D. W. Pyle and M. H. Gromko, *Experientia* 34, 449 (1978); G. Lefevre and U. B. Jonsson, *Genetics* 47, 1719 (1962).
3. J. T. Patterson and W. S. Stone, *Evolution in the Genus Drosophila* (Macmillan, New York, 1952).
4. Fifty eggs were placed in shell vials containing 1.5 g of food medium made up with 50 μ Ci of a mixture of ³H-labeled amino acids (ICN20063).
5. Body parts from three females were pooled in a single scintillation vial containing 100 μ l of ScintiGest tissue solubilizer. Tissues were crushed with glass rods and allowed to digest for 24 hours at 50°C. Glacial acetic acid (2.5 μ l) was added to neutralize the solution. Five milliliters of ScintiVerse I scintillation fluid was then added, and each vial was allowed to sit for an additional 24 hours.
6. M. H. Gromko *et al.*, in *Sperm Competition in Insects*, R. L. Smith, Ed. (Academic Press, New York, in press); R. F. Rockwell, personal communication; W. B. Heed, personal communication.
7. C. L. Boggs and L. E. Gilbert, *Science* 206, 83 (1979); C. L. Boggs, *Evolution* 35, 931 (1981); and W. B. Watt, *Oecologia (Berlin)* 50, 320 (1981).
8. T. A. Markow, M. Quaid, S. Kerr, *Nature (London)* 276, 821 (1978).
9. W. B. Heed, personal communication.
10. J. S. F. Barker and W. T. Starmer, Eds., *Ecological Genetics and Evolution: The Cactus-Yeast-Drosophila Model System* (Academic Press, Sydney, 1982); B. Shorrocks, in *The Genetics and Biology of Drosophila*, M. Ashburner, H. L. Carson, J. N. Thompson, Jr., Eds. (Academic Press, London, 1982) vol. 3b, pp. 385-425; M. Begon, in *ibid.*, pp. 345-381; M. Ashburner, in *ibid.*, vol. 3a, pp. 375-421.
11. G. W. Snedecor and W. G. Cochran, *Statistical Methods* (Iowa State Univ. Press, Ames, 1967), p. 115.
12. We thank Drs. Robert Gemmill and Carol Boggs for technical advice. Supported by NIH grant GM30638-01 (T.A.M.).

24 October 1983; accepted 23 January 1984

Monoclonal Antibody to Thy-1 Enhances Regeneration of Processes by Rat Retinal Ganglion Cells in Culture

Abstract. *Ganglion cells were dissociated from postnatal rat retinas, identified by specific fluorescent labels, and maintained in culture on a variety of substrates. Regeneration of processes by retinal ganglion cells was enhanced when the cells were plated on glass coated with a monoclonal antibody against the Thy-1 determinant. Plain glass and glass coated with polylysine, collagen, fibronectin, or other monoclonal antibodies supported the growth of neural processes, but were less effective than antibody to Thy-1.*

Detailed studies of differentiated mammalian neurons would be aided by examining identified cells in vitro. This approach requires that viable cells be isolated, unequivocally identified, and cultured. Like other neurons of the central nervous system (CNS), mammalian retinal ganglion cells normally do not regenerate their axons after transection, and indeed many of the cells degenerate (1). It is important, therefore, to know whether differentiated retinal ganglion cells can survive and regenerate processes in culture.

Since ganglion cells are the only retinal cells that project to other areas of the CNS, they can be labeled by retrograde transport of markers injected into their projection sites, such as the superior colliculus and lateral geniculate nucleus (2). In histological sections Thy-1 anti-

gen is located on cells and processes in the inner retina and can be used to specifically identify the ganglion cells in vitro (2, 3). Thy-1 is also expressed on the surface of many neurons not found in the retina as well as on T lymphocytes and embryonic muscle (4). Because of sequence homology with immunoglobulins, it has been suggested that molecules displaying the Thy-1 antigen play a role in cellular recognition and morphogenesis in the nervous system (4).

In this report we describe aspects of the identification and growth of solitary rat retinal ganglion cells in culture. MacLeish *et al.* (5) observed that salamander neurons could be grown and maintained on antibody-coated glass cover slips; we tried this method with several antibodies. Comparing growth on different substrates, we found that, by the second day