

Bruce D. Goldman
Curriculum Vitae

Date of Birth: December 11, 1940
Place of Birth: Gary, Indiana

Education:

<u>Institution</u>	<u>Degree</u>	<u>Year</u>	<u>Field</u>
University of Michigan, Ann Arbor	B.S.	1962	Zoology
University of Wisconsin, Madison	M.S.	1966	Zoology
Medical College of Georgia, Augusta	Ph.D.	1968	Endocrinology
University of Texas Medical School, Dallas	Postdoc.	1969	Endocrinology
University of California, Los Angeles	Postdoc.	1970	Neuroendo- crinology

Research and Professional Experience:

2003-present	Professor Emeritus, Department of Physiology and Neurobiology and Department of Ecology and Evolutionary Biology, University of Connecticut
1987-2003	Professor, Department of Physiology and Neurobiology, University of Connecticut
1981-1987	Senior Scientist, Worcester Foundation for Experimental Biology
1979-1980	Professor, Department of Biobehavioral Sciences, University of Connecticut
1975-1979	Associate Professor, Department of Biobehavioral Sciences, University of Connecticut
1970-1975	Assistant Professor, Department of Biobehavioral Sciences, University of Connecticut
1969-1970	Postdoctoral Research Associate, UCLA School of Medicine (with Dr. Roger A. Gorski)
1968-1969	Postdoctoral Research Associate, University of Texas Medical School at Dallas (with Dr. John C. Porter)

Major Research Interests: Neuroendocrinology, Biological Rhythms

Honors:

Member, Endocrinology Study Section (NIH), 1975-1979
Member, Biopsychology Study Section (NIH), 1983-1987
Associate Editor, *Journal of Biological Rhythms*, 1985-1995

PUBLICATIONS

1. Goldman BD and Mahesh VB 1968. Fluctuations in pituitary FSH during the ovulatory cycle in the rat and a possible role of FSH in the induction of ovulation. *Endocrinology* 83:97-106
2. Goldman BD and Mahesh VB 1969. A possible role of acute FSH-release in ovulation in the hamster, as demonstrated by utilization of antibodies to LH and FSH. *Endocrinology* 84:236-243
3. Goldman BD, Kamberi IA, Siiteri PK and Porter JC 1969. The temporal relationship of progesterin secretion, LH release and ovulation in rats. *Endocrinology* 85:1137-1143
4. Porter JC, Goldman BD and Wilber JF 1969. Hypophysiotropic hormones in portal vessel blood. Proceedings of the Workshop on Bioassay and Chemistry of the Hypophysiotropic Hormones of the Hypothalamus, Tuscon, Arizona, January 8-11
5. Goldman BD and Mahesh VB 1970. Induction of infertility in male rats by treatment with gonadotropin antiserum during neonatal life. *Biol Reprod* 2:444-451
6. Goldman BD and Porter JC 1970. Serum LH levels in intact and castrated golden hamsters. *Endocrinology* 87:676-679
7. Porter JC, Kamberi IA, Goldman BD, Mical RS and Grazia YR 1970. The role of substances in the affluent blood supply to the adenohypophysis and in the third ventricular fluid and the release of the luteinizing hormone. *J Reprod Fert* (Suppl) 10:39-49
8. Goldman BD, Grazia YR, Kamberi IA and Porter JC 1971. Serum gonadotropin concentrations in intact and castrated neonatal rats. *Endocrinology* 88:771-776
9. Goldman BD, Mahesh VB and Porter JC 1971. The role of the ovary in control of cyclic LH release in the hamster, *Mesocricetus auratus*. *Biol Reprod* 4:57-65
10. Goldman BD and Gorski RA 1971. Effects of gonadal steroids on the secretion of LH and FSH in neonatal rats. *Endocrinology* 89:112-115
11. Gallo RV, Johnson JH, Goldman BD, Whitmoyer DI and Sawyer CH 1971. Effects of electrochemical stimulation of the ventral hippocampus on hypothalamic electrical activity and pituitary gonadotropin secretion in female rats. *Endocrinology* 89:704-713
12. Goldman BD, Quadagno D, Shryne J and Gorski RA 1972. Modification of phallus development and sexual behavior in rats treated with gonadotropin antiserum neonatally. *Endocrinology* 90:1025-1031
13. Goldman BD and Zarrow MX 1973. The physiology of progestins. In: *Handbook of Physiology, Endocrinology II, Part 1*, pp. 547-572.

14. Goldman BD 1974. The hypothalamic-pituitary-gonadal axis and the regulation of cyclicity and sexual behavior. Neurosciences Research Program, Third Intensive Study Program, MIT Press, Cambridge, MA, pp. 587-591
15. McCullough J, Quadagno DM and Goldman BD 1974. Neonatal gonadal hormones: Effect on maternal and sexual behavior in the male rat. *Physiol Behav* 12:183-188
16. Licht P, Papkoff H, Goldman BD, Follett BK and Scanes CG 1974. Immunological relatedness among reptilian, avian and mammalian pituitary luteinizing hormones. *Gen Comp Endocrinol* 24:168-176
17. Bridges RS, Zarrow MX, Goldman BD and Denenberg VH 1974. A developmental study of maternal responsiveness in the rat. *Physiol Behav* 12:149-151
18. Goldman BD and Sheridan PJ 1974. The ovulatory surge of gonadotropin and sexual receptivity in the female golden hamster. *Physiol Behav* 12:991-995
19. Bridges RS, Goldman BD and Bryant LP 1974. Serum prolactin concentrations and the initiation of maternal behavior in the rat. *Horm Behav* 5:219-226
20. Bridges RS and Goldman BD 1975. Ovarian control of prolactin secretion during late pregnancy in the rat. *Endocrinology* 97:496-498
21. Goldman BD, Bridges RS and Quadagno DM 1975. Sexual Differentiation and patterns of sexual and maternal behavior in the rat: Role of neonatal gonadotropins and gonadal steroids. In: *Sexual Behavior: Pharmacology and Biochemistry*, M. Sandler and G.L. Gessa (eds.), Raven Press, New York, pp. 219-226
22. Quadagno DM, Wolfe HG, Ho GKW and Goldman BD 1975. Influence of neonatal castration or neonatal anti-gonadotropin treatment on fertility, phallus development and male sexual behavior in the mouse. *Fertil Steril* 26:939-944
23. Hutchison JS and Goldman BD 1975. The relationship between the rate of testosterone infusion and gonadotropin secretion. *Endocrinology* 97:725-730
24. Bex FJ and Goldman BD 1975. Serum gonadotropins and follicular development in the Syrian hamster. *Endocrinology* 96:928-933
25. Seegal RF and Goldman BD 1975. Effects of photoperiod on cyclicity and serum gonadotropins in the Syrian hamster. *Biol Reprod* 12:223-231
26. Bridges RS and Goldman BD 1975. Diurnal rhythms in gonadotropins and progesterone secretion in lactating and photoperiod induced acyclic hamsters. *Biol Reprod* 13:617-622
27. Bridges RS and Goldman BD 1976. Suckling and LH-induced progesterone secretion in lactating hamsters (*Mesocricetus auratus*). *Neuroendocrinology* 21:20-30

28. Bridges RS, Tamarkin L and Goldman B 1976. Effects of photoperiod and melatonin on reproduction in the Syrian hamster. *Ann Biol Anim Bioch Biophys* 16:339-408
29. Tamarkin L, Westrom WK, Hamill AI and Goldman BD 1976. Effect Of melatonin on the reproductive systems of male and female Syrian hamsters: A diurnal rhythm in sensitivity to melatonin. *Endocrinology* 99:1534-1541
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31. Selmanoff MK, Goldman BD and Ginsburg BE 1977. Developmental changes in serum luteinizing hormone, follicle stimulating hormone and androgen levels in males of two inbred mouse strains. *Endocrinology* 100:122-127
32. Bex FJ and Goldman BD 1977. Serum gonadotropins associated with puberty in the female Syrian hamster. *Biol Reprod* 16:557-560
33. Barkley MS and Goldman BD 1977. A quantitative study of serum testosterone, sex accessory organ growth, and the development of intermale aggression in the mouse. *Horm Behav* 8:208-218
34. Barkley MS and Goldman BD 1977. Testosterone induced aggression In adult female mice. *Horm Behav* 9:76-84
35. Selmanoff MK, Goldman BD, Maxson SC and Ginsburg BE 1977. Correlated effects of the Y-chromosome of mice on developmental changes in testosterone levels and intermale aggression. *Life Sciences* 20:359-366
36. Tamarkin L, Hollister CW, Lefebvre NG and Goldman BD 1977. Melatonin induction of gonadal quiescence in pinealectomized Syrian hamsters. *Science* 198:953-955
37. Tamarkin L, Lefebvre NG, Hollister CW and Goldman BD 1977. Effect of melatonin administered during the night on reproductive function in the Syrian hamster. *Endocrinology* 101:631-634
38. Selmanoff MK, Goldman BD and Ginsburg BE 1977. Serum testosterone, agonistic behavior, and dominance in inbred strains of mice. *Horm Behav* 8:107-119
39. Selmanoff MK, Abreu E, Goldman BD and Ginsburg BE 1977. Manipulation of aggressive behavior in adult DBA2/Bg and C5BL/10/Bg male mice implanted with testosterone in silastic tubing. *Horm Behav* 8:377-390
40. Bartke A, Goldman BD, Bex F and Dalterio S 1977. Effects of prolactin (PRL) on pituitary and testicular function in mice with hereditary PRL deficiency. *Endocrinology* 101:1760-1766

41. Goldman BD 1978. Developmental influences of hormones on neuroendocrine mechanisms of sexual, maternal and aggressive behaviours. In: *Biological Determinants of Sexual Behaviour*, J.B. Hutchison (ed.), John Wiley & Sons, New York, pp. 127-152.
42. Barkley MS and Goldman BD 1978. Studies on opponent status and steroid mediation of aggression in female mice. *Behav Biology* 23:118-123.
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53. Margules DL, Goldman B and Finck A 1979. Hibernation: An opioid-dependent state? *Brain Res Bull* 4:721-724.

54. Goldman BD 1980. Seasonal cycles in testis function in two hamster species: Relation to photoperiod and hibernation. In: *Testicular Development, Structure, and Function*, A. Steinberger and E. Steinberger (eds.), Raven Press, New York, pp. 401-409.
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57. Hall V and Goldman B 1980. Effects of gonadal steroid hormones on hibernation in the Turkish hamster (*Mesocricetus brandti*). *J Comp Physiol* 135:107-114.
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59. Erskine MS, Barfield RJ and Goldman BD 1980. Postpartum aggression in rats. II. Dependence on maternal sensitivity to young and effects of experience with pregnancy and parturition. *J Comp Physiol Psychol* 94:495-505.
60. Bartke A, Goldman BD, Klemcke HG, Bex FJ and Amador AG 1980. Effects of photoperiod on pituitary and testicular function in seasonally breeding species. In: *Functional Correlates of Hormone Receptors in Reproduction*, V. Mahesh, T. Muldoon, B. Saxena and W. Sadler (eds.), Elsevier, Amsterdam, pp. 171-185.
61. Bartke A, Goldman BD, Bex FJ, Kelch RP, Smith MS, Dalterio S and Doherty PC 1980. Effects of prolactin on testicular regression and recrudescence in the golden hamster. *Endocrinology* 106:167-172.
62. Goldman BD, Matt KS, Roychoudhury P and Stetson MH 1981. Prolactin release in golden hamsters: Photoperiod and gonadal influences. *Biol Reprod* 24:287-292.
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78. Carter DS and Goldman BD 1983. Antigonadal effects of timed melatonin infusion in pinealectomized male Djungarian hamsters (*Phodopus sungorus sungorus*): duration is the critical parameter. *Endocrinology* 113:1261-1267.

79. Carter DS and Goldman BD 1983. Progonadal role of the pineal in the Djungarian hamster (*Phodopus sungorus sungorus*): mediation by melatonin. *Endocrinology* 113:1268-1273.
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103. Darrow JM, Tamarkin L, Duncan MJ and Goldman BD 1986. Pineal melatonin rhythms in female Turkish hamsters: Effects of photoperiod and hibernation. *Biol Reprod* 35:74-83.
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Previous Extramural Grants Awarded:

Reproductive Hierarchy and Sexual Differentiation, NSF, 4/1/04-3/31/07, \$50,201 direct costs for 2004-05.

Neural Sites of Melatonin Action and Biological Rhythms, NIMH, 6/1/94-5/31/00, \$297,578 direct costs

Neuroendocrine Factors in Hibernation, NSF, 3/1/91-8/31/95, \$184,085 direct costs

Endocrine Regulation of Annual Pelage Cycle, PHS, 2/1/86-1/31/89, \$264,461 direct costs (This award was initiated while the PI was at the Worcester Foundation. It was transferred to the University of Connecticut in 1987.)

Environmental and Hormonal Factors in Hibernation, PHS, 1/1/83-12/31/87 (This award was initiated while the PI was at the Worcester Foundation. It was transferred to the University of Connecticut in 1987.)

Photoperiodic Regulation of Mammalian Reproduction, PHS, 4/1/86-3/31/91, \$598,522 (This award was initiated while the PI was at the Worcester Foundation. It was transferred to the University of Connecticut in 1987.)

Photoperiodic Regulation of Mammalian Reproduction, PHS, 4/1/81-3/31/86, \$321,718 direct costs

Environmental and Hormonal Factors in Hibernation, PHS, 1/1/80-12/31/82, \$169,841 direct costs

Photoperiodic Regulation of Mammalian Reproduction, PHS, 9/1/77-8/31/81

Environmental and Hormonal Factors in Hibernation, PHS, 10/1/76-9/30/79, \$90,735 direct costs

Control of Pituitary and Gonadal Hormone Secretion, PHS, 1/1/71-12/31/73, \$96,665 direct costs

National Review Boards:

Endocrinology Study Section, NIH (1975/79)

Biopsychology Study Section, NIH (1983/87)

Editorships (current):

Editorial Board, Journal of Pineal Research

Editorial Board, Journal of Biological Rhythms (2001-current)

Editorships (past):

Editorial Board, American Journal of Physiology

Associate Editor, Journal of Biological Rhythms (1985-1994)
Editorial Board, Hormones and Behavior (1986-1996)
Editorial Board, Neuroendocrinology

Courses taught:

Biological Rhythms (PNB 225/325)
Hormones and Behavior (PNB 230/330)
Topics in Modern Biology (Biol 196)
Foundations of Biology (Biol 107)
Comparative Endocrinology (PNB 421, with Drs. Nancy Clark and David
Borst)
Comparative Endocrinology Laboratory (PNB 422)
Behavioral Endocrinology (EEB 297)
Animal Models and Human Evolution (EEB 210)

Research of Bruce D. Goldman

The following areas of research have been studied in the laboratory of Bruce Goldman. Following a description of each area is a list of the related publication numbers, as listed in my Curriculum Vitae:

- 1) Patterns of secretion of pituitary gonadotropins and their role in ovulation in rats and Syrian hamsters (Ph.D. dissertation; publications 1-4,6,7,9,11,14,24,32,45)

Serum concentrations of both LH and FSH increase sharply a few hours prior to ovulation in rats and hamsters. Injections of either of these hormones induced ovulation in females with mature ovarian follicles. Treatment of females with antibodies formed against FSH and LH, respectively, revealed that both hormones are released in quantities that are adequate to trigger ovulation.

I also examined the role of FSH in the early recruitment of ovarian follicles. My studies supported the importance of a transient rise in plasma FSH concentration for triggering the process of follicular maturation that ultimately culminates with ovulation.

- 2) Role of pituitary and testicular hormones in sexual differentiation during neonatal life in rats; serum concentrations of gonadotropins in neonatal rats (Ph.D. dissertation; publications 5,8,10,12,15,21,22,41,124)

It has been very clearly established that testis hormones (androgens) are essential to masculinization of a number of physiological and behavioral systems during mammalian development. In many rodents, sexual differentiation of these systems occurs at about the time of birth. Our studies revealed that the neonatal rat testis is under regulation by pituitary gonadotropins (FSH and LH). Treatment of neonatal male rats with antisera to FSH and LH resulted in partial blockade of masculinization, an effect that persisted into adulthood. We verified for the first time that neonatal rats actively secrete FSH and LH. Serum concentrations of these hormones are higher in newborn females as compared to males. Serum FSH and LH concentrations increased following castration in neonatal males, and levels of these hormones were decreased when the neonates were treated with androgen or estrogen.

- 3) Hormones and maternal behavior in rats (publications 17,19,20,27)
- 4) Secretion patterns and regulation of pituitary gonadotropin secretion and testicular androgen secretion in male rats and mice (publications 23,31,52,113)
- 5) Hormones and aggression in rats and mice (publications 33,35,38,39,42-44,58,59)
- 6) Hormones, pheromones and sexual behaviors in Syrian hamsters (publications 18,91)

- 7) Role of photoperiod, the pineal gland, and melatonin in the regulation of seasonal changes in reproduction in Syrian hamsters, Turkish hamsters, Siberian hamsters, and laboratory rats (publications 25, 26, 28-30, 36, 37, 46-51, 54-56, 60-64, 68, 71, 72, 74-79, 81-83, 85, 94, 98, 99, 103, 108, 111, 115, 116, 121-123, 125-127, 129, 131-133, 135-138, 142, 143, 145, 146, 148, 149, 152-154, 156, 158, 159)

My laboratory was involved in the study of pineal function and photoperiodism in mammals for approximately 24 years. We were the first group to report that timed daily injections of the pineal hormone, melatonin (MEL), could 'mimic' several of the actions of short day lengths on the reproductive system in pineal-intact Syrian hamsters. We also reported that multiple daily injections of MEL could product the same effects in pinealectomized hamsters. These observations provided the first strong evidence that MEL is the pineal hormone involved in photoperiodic regulation of reproduction. By extending our studies of pineal physiology to several other mammal species, we and others have demonstrated that MEL is involved in the seasonal (photoperiodic) regulation of numerous functions in addition to reproductive activity. For example, in Siberian hamsters, photoperiod-driven changes in MEL secretion are central to the seasonal changes in pelage, lipid metabolism, body weight, and thermoregulation.

By carrying out a series of studies employing the paradigm of timed daily infusions of MEL in pinealectomized hamsters, we were the first to demonstrate the specific nature of the 'photoperiod signal'. These experiments revealed the overriding importance of the duration of each (circadian) episode of MEL. Additional studies revealed the fundamental importance of day length, acting through the circadian system, in regulating the duration of nightly episodes of MEL biosynthesis/secretion. Other laboratories have confirmed this model of pineal MEL function in various species, including sheep, mink, ferrets, mice, deer, and wallabies.

Later studies in my laboratory revealed that MEL acts in at least three separate brain sites to exert its actions on the hamster reproductive system. We also showed that for Siberian hamsters, individual variations in response to photoperiod are a function of differences in properties of the circadian system. These variations have a heritable basis, but they are also subject to major environmental influence; thus, major changes in photoresponsiveness can occur during an individual's life history.

- 8) Gonadal hormones, hibernation, and daily torpor in Turkish hamsters, European hamsters, and Siberian hamsters (publications 53, 57, 70, 73, 96, 104, 106, 107, 112, 114, 117, 120, 134)

During approximately 19 years of study, my laboratory examined relationships between reproductive hormones and winter torpor (hibernation and daily torpor) in three species of hamsters. These studies revealed that increased levels of testosterone abruptly terminate torpor. We proposed that this endocrine mechanism might serve to help coordinate the end of the hibernation season with the seasonal onset of reproduction. Thus, hibernation will be terminated just as the testes begin to exhibit endocrine activity, assuring that males will become reproductively competent soon after

emergence from hibernation. In support of this hypothesis, we observed that castrated male hamsters remained in hibernation for several weeks beyond the time when hibernation had terminated in testis-intact males. We also reported that seasonal patterns of hormone secretions (FSH, LH, prolactin, testosterone) are expressed in hibernating hamsters similarly to the patterns seen in individuals that are not allowed to hibernate; thus, seasonal timing mechanisms are not seriously disrupted during hibernation.

- 9) Role of photoperiod, melatonin, and prolactin in seasonal pelage changes and in lipid metabolism in Siberian hamsters (publications 86,87,92,93,109,119)

Many Temperate Zone mammals exhibit seasonal pelage changes, typically with a fall molt to a strongly insulating pelage and a spring molt to return to a summer coat. Studies in my laboratory, using Siberian hamsters, revealed that the type of fur produced following a molt (summer or winter fur) is determined by the circulating concentration of prolactin. High levels of prolactin--typically in effect during the summer (long day lengths) result in growth of a summer coat, whereas low levels of prolactin (short day lengths) lead to the growth of winter pelage. In other laboratories, this mechanism has been confirmed for several other species, including fox, deer, and mink.

- 10) Role of prolactin in regulation of testis function in Syrian hamsters and mice (publications 40,69,84,90,130)
- 11) Transfer of photoperiod information from mother to fetus in Siberian hamsters (publications 97,102,118,139-141,157)

The photoperiod in effect during gestation influences the photoperiod responsiveness of hamster pups, as exhibited beginning at about two weeks postpartum. Our studies revealed that a 'photoperiod message' is transmitted by the mother to her fetuses. This message is provided in the form of the mother's rhythm of pineal MEL secretion.

We also investigated the mechanism by which the maternal MEL rhythm alters photoperiod responses of her offspring. Our data indicate that the pineal MEL rhythms of 2-week-old hamsters were differentially affected by the photoperiods experienced by their mothers (and the mothers' corresponding MEL rhythms) during gestation. Interestingly, this influence of the mother was observed only in male, and not in female, pups.

- 12) Circadian rhythms: influence of environmental factors, maternal influence, endocrine influences---hamsters and mole-rats (publications 80,88,95,100,101,110,128,144,150,151)

My laboratory has carried out several studies examining the physiology of the circadian system in mammals. Most recently, we have been the only laboratory to carry out systematic studies of circadian function in subterranean mammals. The subjects for these studies have been two species that are almost exclusively

fossorial---the blind mole-rat and the naked mole-rat. Both species exhibit circadian rhythms of locomotor activity and body temperature that are entrainable by light cues.

- 13) Sexual differences and sexual differentiation in naked mole-rats and Damaraland mole-rats (publications 155, 160-169)

In collaboration with Drs. Nancy Forger and Geert DeVries (University of Massachusetts, Amherst) I am studying sex differences in behavior and the nervous system in naked mole-rats. This eusocial species exhibits an absence of sex differences in several features that are sexually different in most other mammals; perhaps most notably, there is no sex difference in cell numbers or cell size in Onuf's nucleus of the spinal cord (homologous to the spinal nucleus of the bulbocavernosus) or in the major perineal muscles. We have proposed that the decreased degree of sex difference in this species may have evolved in conjunction with the social/reproductive structure of naked mole-rats, with only one breeding female and 1-3 breeding males in each colony (typical colony size of 60-80 individuals). We will pursue this research in naked mole-rats and in closely related species that show different degrees of reproductive skew, ranging from species that are similarly eusocial but with smaller colony sizes to species.

Our most recent research in a second eusocial rodent, the Damaraland mole-rat, has demonstrated that both sexes continue to exhibit sex behaviors (mounting by males, solicitation and lordosis by females) for at least several months after gonadectomy. Preliminary results suggest that sex behaviors are exhibited post-gonadectomy even by individuals that had no sexual experience before surgery.