on the coremata is derived (as in *Utetheisa*) from defensive pyrrolizidine alkaloids sequestered in the larval food plants (*2*). The morphogenesis and pheromone content of the coremata are influenced by the dietary alkaloid so that females might be able to directly assess the alkaloid content—that is, the degree of chemical protectiveness—of the males by the size of their coremata, the pheromone content, or both. However, neither *Creatonotos* nor *Utetheisa* are known to form leks.

If a similar situation occurs in *E. acrea*, females visiting leks may be able to assess the fitness of assembled males, although we never observed females to move from one male to another: they flew straight in and mated with the first displaying male contacted. Unlike *Creatonotos*, however, *E. acrea* shows no readily discernible natural variation in the size of male coremata with diet, and the larvae feed on a wide range of garden and crop plants without any apparent deleterious dietary effects (*16*).

Male leks have not been well substantiated in the Lepidoptera, especially moths, nor has the use of male brushes or coremata in long-range attraction. Furthermore, the occurrence of a dual system of mating, one based on female attraction and the other on male attraction, in the same species (and population) has apparently not been reported. What sort of stimuli are provided by the coremata and by the lek as a whole, and what sort of selection pressures led to the evolution and maintenance of both strategies in this species is not known.

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References and Notes

1. M. C. Birch, *Pheromones* (Elsevier, New York, 1974), p. 115; R. L. Rutowski, *J. Comp. Physiol.* **115**, 75 (1977); T. C. Baker and R. T. Cardé, *Ann. Entomol. Soc. Am.* **72**, 173 (1979).
2. H. T. Pagden, *Proc. R. Entomol. Soc. London Ser. A* **32**, 90 (1957); G. Robinson, in G. C. Varley, *Trans. Soc. Br. Entomol.* **15**, 29 (1962); D. Schneider, M. Boppré, J. Zweig, S. B. Horsley, T. W. Bell, J. Meinwald, K. Hansen, E. W. Diehl, *Science* **215**, 1264 (1982).
3. W. E. Conner, T. Eisner, R. K. Vander Meer, A. Guerrero, J. Meinwald, *Behav. Ecol. Sociobiol.* **9**, 227 (1981).
4. M. C. Birch, in *Moths and Butterflies of Great Britain and Ireland*, vol. 9, *Sphingidae-Noctuidae*, J. Heath and A. M. Emmet, Eds. (Curwen, London, 1979), p. 9.
5. H. K. Morrison, *Psyche* **1**, 21 (1874); R. H. Stretch, *Papilio* **3**, 41 (1883); C. D. MacNeill, *Pan-Pacif. Entomol.* **38**, 195 (1962). Each describes the eversion of coremata by a single male, either without describing the circumstances, or at artificial light.
6. A. S. Hill and W. L. Roelofs, *J. Chem. Ecol.* **7**, 655 (1981).
7. Mating stations were metal pans 40 cm in diameter with a 10-cm rim and with a vertical cloth supported in the center, 20 cm high, on which males and females would display. Both wings on one side of males and females were amputated to prevent flight. Virgin males and females were reared in the laboratory on a lima bean–based diet [after H. H. Shorey and R. L. Hale, *J. Econ. Entomol.* **55**, 522 (1965)]. Mating stations were placed 40 m apart in alfalfa as part of a set, which consisted of a natural aggregation, a mating station with five males, a mating station with five females, a control (empty mating station), and a pheromone trap [A. W. Hartstack, J. A. Witz, C. R. Buck, *J. Econ. Entomol.* **72**, 519 (1979)]. To compare and analyze data between experiments and observations on different nights, the data from aggregations, mating stations, and pheromone traps were converted to percentages. The total recorded for each treatment (number of displaying males, number of trapped males, and so on) in any night was set as 100, and the number obtained for this category in each half-hour period was then calculated as a percentage of this total. The means of these percentages were used as an indication of the amount of that particular activity for each period. Total numbers of males and females initiating mating in each period were compared by the Mann-Whitney *U* test.
8. J. A. Scott, *J. Res. Lepid.* **11**, 99 (1972); R. J. Bartell, in *Chemical Control of Insect Behavior*, H. H. Shorey and J. J. McKelvey Jr., Eds. (Wiley, New York, 1977), p. 201.
9. Males of the greater and lesser wax moths, *Galleria mellonella* and *Achroia grisella* (Pyralidae), attract females over a distance, reported to be a "long distance," but unspecified [H. Röller, K. Biemann, J. S. Bjerke, D. W. Norgard, W. H. McShan, *Acta Entomol. Bohemoslov.* **65**, 208 (1968); K. H. Dahm, D. Meyer, W. E. Finn, V. Reinhold, H. Röller, *Naturwissenschaften* **58**, 265 (1971); W. E. Finn and T. L. Payne, *Southwest. Entomol.* **2**, 62 (1977)].
10. T. C. Baker, R. Nishida, W. L. Roelofs, *Science* **214**, 1359 (1981). A blend of three pheromones identified from the hair pencils of males attracts sex pheromone–releasing females from several centimeters, after males have been attracted into their vicinity by the female pheromone.
11. Similar behaviors almost certainly exist in the Hepialidae [C. G. Barrett, *Entomol. Mon. Mag.* **19**, 90 (1882); J. E. Robson, *ibid.* **23**, 186 (1887); A. G. Carolsfeld-Krausé, *Entomol. Rec. J. Var.* **71**, 33 (1959); Cadbury, in B. Kettlewell, *The Evolution of Melanism* (Clarendon, Oxford, 1973)], p. 296.
12. D. McFarland, Ed., *The Oxford Companion to Animal Behaviour* (Oxford Univ. Press, Oxford, 1981), p. 346; R. D. Alexander, in *Insects, Science and Society*, D. Pimental, Ed. (Academic Press, New York, 1975), pp. 35–77; G. A. Parker, *Annu. Rev. Entomol.* **23**, 173 (1978); N. B. Davies, in *Behavioural Ecology*, J. R. Krebs and N. B. Davies, Eds. (Blackwell, Oxford, 1978), p. 332; J. W. Bradbury, in *Natural Selection and Social Behaviour*, R. D. Alexander and E. W. Tinkle, Eds. (Chiron, New York, 1981), p. 138.
13. For example, hilltopping (aggregations typically on hilltops) in butterflies [O. Shields, *J. Res. Lepid.* **6**, 69 (1967)]; temporal leks in dragonflies [P. J. Campanella and L. L. Wolf, *Behaviour* **51**, 4 (1974)]; euglossine bees [L. S. Kimsey, *Anim. Behav.* **28**, 996 (1980)]; and Hawaiian *Drosophila* [H. T. Spieth, *Annu. Rev. Entomol.* **19**, 385 (1974)]; various unpublished or anecdotal references [M. D. Greenfield, *Florida Entomol.* **64**, 4 (1981)]; and (possibly) swarms of many species of flies [H. Oldroyd, *The Natural History of Flies* (Wiedenfeld & Nicholson, London, 1964)].
14. The two behavior patterns may form a mixed or a conditional strategy for mating [R. Dawkins, in *Sociobiology: Beyond Nature/Nature?*, G. W. Barlow and J. Silverberg, Eds. (Westview Press, Boulder, Colo., 1980), p. 331].
15. In the arctiid, *Hyphantria cunea*, location of females by males may be based more on visual cues from the brilliant white female in the calling posture than by the female pheromone, which has a more localized effect [T. Hidaka, *Appl. Entomol. Zool.* **7**, 116 (1972)].
16. C. L. Metcalf, W. P. Flint, R. L. Metcalf, *Destructive and Useful Insects* (McGraw-Hill, New York, ed. 4, 1962).
17. We thank K. F. Haynes, R. W. Hall, S. S. Duffey, and P. H. Sterling for stimulating discussions and assistance and R. Dawkins for helpful comments on the manuscript.
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Ecological Correlates of Paternal Investment of Urates in a Tropical Cockroach

Abstract. *Females of the tropical cockroach* Xestoblatta hamata *feed on urates offered by the male after copulation. Females on nitrogen-deficient diets ingest and transfer to their maturing oocytes more male-derived uric acid than do females on high-protein diets. In isolated females, the greatest uptake of uric acid by the ovaries occurs during the mating stage in the reproductive cycle. Uric acid from males contributes significantly to the female's nitrogen pool and may help shorten the time between mating and oviposition. In both field and laboratory experiments males choose high-protein foods and dietary uric acid.*

Cockroaches, unlike many terrestrial insects, void little uric acid (*1*). Instead, they store urates in specialized cells of the fat body or secrete them into accessory glands in males of some species. In three subfamilies of cockroaches the male coats his sperm package with uric acid after inserting it into the female (*2*). Roth (*3*) suggested that uric acid might protect the spermatophore from being prematurely consumed by the female or by other insects, and Cornwell (*4*) that it might act like a plug to prevent females from mating repeatedly. Mullins and Keil (*5*) reported, however, that the spermatophore-urate complex may disappear shortly after mating and that male uric acid could be recovered from mated *Blattella germanica* females and their oothecae. They found that the transfer of the urates was related to the nutritional state of the female: those on a low-protein diet transferred more to oothecae than did those on a high-protein diet. Mullins and Keil (*5*) suggested that the transfer of urates might represent "paternal investment of a nitrogen resource from which the female and her progeny might benefit."

We report a postcopulatory behavior in the tropical rain-forest cockroach *Xestoblatta hamata* that supports the paternal investment proposal (*6*). After copulation the male raises his wings, tele-

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scopes his abdomen, widens the genital chamber exposing a white urate secretion, and directs it toward the female (Fig. 1B), who ingests the secretion. This behavior supports the nutritional investment hypothesis and Mullins and Keil's suggestion that male urates are ingested by the female (*B. germanica* in their report, subfamily Blattellinae, as is *X. hamata*). This is one of few cockroach species for which sufficient ecological data are available (7) to directly assess the significance of male dietary contributions to the female's nitrogen budget.

Both the size of the male's uricose glands and the dietary nitrogen status of the female determine the duration of feeding and the quantity of uric acid ingested by the female. We maintained some males and females on an 8 percent casein protein diet and others on a 64 percent casein diet; in males the result was small (mean ± S.E.M., 13.0 ± 1.5 mg; $N = 9$) and large (27.4 ± 1.2 mg; $N = 11$) uricose glands, respectively, after 20 days. Long, uninterrupted postcopulatory feeding was common when the male had large stores of urates regardless of the nutritional condition of the female (pooled data for both female groups: 216.5 ± 19.23 seconds, 2.3 ± 0.33 pauses; $N = 11$). Females deficient in dietary nitrogen ($N = 5$) continued to palpate the male and attempted to feed after his small gland was depleted. Hence, their cumulative feeding periods were significantly longer than those of females with high dietary nitrogen ($N = 7$): 128.0 ± 22.73 seconds, 4.0 ± 0.45 pauses, versus 76.4 ± 12.66 seconds, 2.9 ± 0.40 pauses ($P < .05$, Mann-Whitney U test).

Females maintained on the low-protein diet incorporated and transferred to their egg cases large quantities of label, which had been injected into males as [8-^{14}C]hypoxanthine, whether the males had small or large uricose glands (Table 1). Females on a high-protein diet acquired significantly less label from males with large uricose glands ($t = 3.53$, $P = .008$) and consequently incorporated less label into their oothecae ($t = 8.67$, $P = .003$) (*8*).

Transfer of uric acid into the terminal oocytes begins after the third night of an 8- to 9-day ovarian cycle; mating usually occurs on the fourth night. As both the protein content (due to uptake of blood vitellogenin) and the mass of the ovaries increase, the percentage of nitrogen content remains relatively constant (8.47 ± 0.51 percent). Yet, ovarian uric acid (uricase assay) increases from 3.4 μg per milligram of dry ovary early in the cycle to 61.7 μg per milligram of dry ovary when ovulation begins. Hence, the percentage of total ovarian nitrogen attibuted to uric acid increases from 1.0 percent immediately after deposition of an egg case (day 1) to 27.7 percent in mature oocytes. A similar pattern was observed by incorporation of labeled hypoxanthine in the ovaries (*9*).

Females mate repeatedly throughout their adult lives either because of sperm shortage or because of urate deficiency. The latter is implicated by the following data: females maintained on a high-protein diet produced egg cases containing significantly more uric acid than females on an 8 percent protein diet (7.6 ± 1.01 μ*M* and 4.8 ± 1.00 μ*M* per egg case, corresponding to 2.58 and 1.52 percent of the dry weights, respectively; $N = 8$, $P = .01$). Two freshly deposited oothecae collected in the field yielded an average of 7.3 μ*M* uric acid, suggesting that, in the forest, females may feed on high-protein foods, on uric acid, or on both. Yet field evidence indicates that females feed on nitrogen-deficient foods and rarely forage on uric acid (*10*). As in the German cockroach, but unlike the American cockroach, *X. hamata* females use most of the food consumed before oviposition for a single egg case; little nutrient storage occurs (*11*). Moreover, in the field, the uric acid content (ovaries and stomachs excluded) of postoviposition females did not differ from females midway through the ovarian cycle (11.51 ± 4.75 μ*M* and 12.23 ± 3.91 μ*M* per female, which represent 1.54 and 1.16 percent of the body dry weight, respectively; $N = 10$, $P = .89$) (*12*), and some females in both groups had low uric acid reserves. An increase in uric acid content through the first 4 days of the ovarian cycle should occur if females ingested foods high in nitrogen.

The average male has sufficient uric acid in his uricose gland to supply enough for ten egg cases, if there is no

Table 1. Fate of labeled hypoxanthine injected into males. Males with empty uricose glands were injected with 1 μl [8-^{14}C]hypoxanthine and maintained on 8 or 64 percent protein diets for 8 to 30 days. The ^{14}C-labeled urates were traced in males, mated whole females, and in egg cases by the extraction and counting procedures of Mullins and Keil (*5*). The amount of label incorporated into the accessory gland increased with time ($y = 6900 \pm 3000x$). Only copulations occurring 20 to 25 days after injection are reported. Uricose glands of unmated males averaged 114,606 ± 19,207 dis/min per male ($N = 7$); the average for the rest of the body was 11,327 ± 588 dis/min ($N = 7$) after 20 to 25 days. The relatively large variance in the radioactivity of females in the group on the 64 percent protein diet with access to large uricose glands was in part due to defecation of uric acid shortly after ingestion. Two white fecal pellets from two females in this group contained 25,817 and 33,511 dis/min per insect. Each entry represents a mean, standard error of the mean, number, and coefficient of variation. Significance values are based on t-tests.

Male gland	Radioactivity (10^3 dis/min)								
	Mated females					Mated males			
	Whole*	P	First ootheca	P	Second ootheca†	Uricose gland	P	Rest of body	P
					8 percent protein diet				
Small	77.2 ± 5.9 (5; 17.2 percent)‡		22.5 ± 2.7 (3; 20.9 percent)		15.8 ± 1.7 (2; 15.4 percent)	12.4 ± 3.1 (5; 56.1 percent)		14.7 ± 1.2 (5; 18.8 percent)	
		.618		.156			.184		.816
Large	73.1 ± 5.0 (5; 15.2 percent)		16.9 ± 2.1 (4; 24.7 percent)		9.3 ± 2.0 (2; 29.8 percent)	20.4 ± 4.5 (5; 49.8 percent)		15.1 ± 1.2 (5; 17.4 percent)	
					64 percent protein diet				
Small	59.3 ± 10.2 (5; 38.5 percent)		8.7 ± 0.6 (2; 9.1 percent)		3.0 (1)	45.4 ± 7.0 (5; 34.6 percent)		14.9 ± 1.2 (5; 18.1 percent)	
		.008		.003			.002		.762
Large	19.5 ± 4.7 (5; 54.4 percent)		2.5 ± 0.4 (3; 30.8 percent)			88.7 ± 6.0 (5; 15.2 percent)		14.3 ± 1.6 (5; 25.7 percent)	
					8 percent versus 64 percent protein diet				
		.001		<.001			<.001		.825

*Extracted 48 hours after copulation. †Females on the 64 percent protein diet produced only one second egg case. ‡The number in parentheses is the sample size and the percentage is the coefficient of variation.

loss during transfer and uptake by the female (*13*). Since oothecal uric acid is related to dietary nitrogen, and if embryonic uric acid increases the fitness of the young, females would have to forage for high-nitrogen foods to obtain adequate quantities of uric acid in the absence of males.

Our data indicate that if females have access to uric acid after mating, the preovipositional period may be shortened. Since delaying oviposition may result either in resorption of oocytes if essential nutrients are not available (*14*) or in remating, or both, the male should minimize the time between mating and oviposition. In *B. germanica* when two males mate with a female before she oviposits, mixing of the two ejaculates (that is, sperm competition) may occur (*15*).

Presumably, these consequences of nitrogen deficiency, short reproductive cycles, a concurrent demand by females for other nutrients, and the relative scarcity of foods high in nitrogen would select for male urate contribution to females. Although males have relatively low nitrogen requirements, they feed on bird and reptilian droppings (Fig. 1C) which are largely uric acid. In choice experiments in the laboratory, males consume large percentages of uric acid and high-protein food which results in rapid enlargement of their uricose glands. Yet, if sexually receptive females are not available to accept the accessory secretion, accumulation of extracellular uric acid results in increased mortality (*16*). Pressures on the male to accumulate and void stored urates and his enhanced fitness when uric acid is successfully transferred to the female may have contributed to the evolution of a relatively protracted copulation (248.3 ± 18.5 minutes; $N = 9$) (*17*). This period approximately corresponds to the time required for the crop to empty following feeding. In the forest, females feed on plant material starting at approximately 1900 hours and couple with males at midnight, allowing for only one mating per night. Hence, the male may be delaying the deposition of a spermatophore until the female's crop is empty and she can accommodate his urate secretion.

On the basis of significant urate accumulation in aposymbiotic cockroaches, and mobilization of urates by cockroaches deficient in nitrogen, researchers have implicated intracellular bacteria in the degradation of uric acid (*18*). Specialized cells harboring symbiotic bacteria are also found in the ovaries of cockroaches (*19*) and are transferred to oocytes during their maturation. If, in fact, transovarial transmission of uricolytic bacteria occurs in *X. hamata* (as it does in the other cockroach species examined thus far), then nitrogen and carbon may be gained from metabolism during embryogenesis of paternally derived uric acid.

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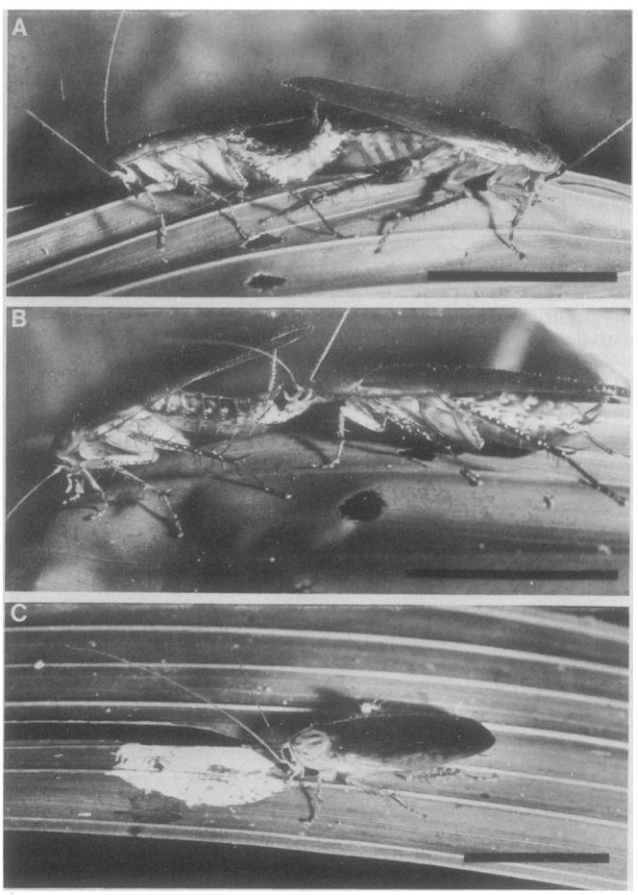

Fig. 1. (A) Copulating pair of *Xestoblatta hamata* perched on a leaf in the understory of a tropical rain forest in Costa Rica. The white uricose gland may be seen through the transparent cuticle in the arched terminal abdominal segments of the male (left). (B) Immediately after separating, the female (right) turns and feeds on urates from the male's uricose gland. (C) Male *X. hamata* feeding on bird droppings on a leaf. Scale bars, 2 cm.

References and Notes

1. D. E. Mullins and D. G. Cochran, *Science* **177**, 699 (1972).
2. L. M. Roth and G. P. Dateo, *ibid.* **146**, 782 (1964); *J. Insect Physiol.* **11**, 1023 (1965).
3. L. M. Roth, *Ann. Entomol. Soc. Am.* **60**, 1203 (1967); *Annu. Rev. Entomol.* **15**, 75 (1970).
4. P. B. Cornwell, *The Cockroach* (Hutchinson, London, 1968).
5. D. E. Mullins and C. B. Keil, *Nature (London)* **283**, 567 (1980).
6. This work was conducted between February and June 1980 and 1981 at Finca La Selva, an Organization for Tropical Studies field station in Costa Rica; see L. R. Holdridge, W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. [*Forest Environments in Tropical Life Zones: A Pilot Study* (Pergamon, Oxford, 1971)] for site description.
7. C. Schal, *Science* **215**, 1405 (1982); ———, G. Y. Gautier, W. J. Bell, in preparation.
8. Some label was lost in the transfer of uric acid. We did not quantify the conversion of hypoxanthine to uric acid nor measure urate metabolism to $^{14}CO_2$. In *Parcoblatta* the amounts of $^{14}CO_2$ evolved are related to nitrogen content in the diet (D.G. Cochran, personal communication).
9. We injected 1 μl of [8-^{14}C]hypoxanthine into females on the first day of the ovarian cycle (postoviposition) and assayed the radioactivity of paired ovaries on subsequent days. The radioactivity was 352 ± 32 dis/min on day 2 ($N = 3$), 5170 ± 1200 dis/min on day 4 ($N = 4$), and 10,479 ± 1148 dis/min ($N = 3$) on day 6. The females were maintained on a 25 percent protein diet.
10. Choice experiments in the laboratory showed that high-nitrogen diets were consumed mainly on nights 3 and 4 of the ovarian cycle. Foods (mainly plant material) ingested at this stage in the field contained more nitrogen than did foods consumed during earlier and later stages, but the nitrogen content was not sufficient to produce the 7 μ*M* or uric acid found in egg cases collected in the field (data not shown).
11. *Blattella germanica* females use 90 percent of the food gained in the preovipositional period for production of a single egg case [J. G. Kunkel, *J. Insect Physiol.* **12**, 227 (1966)].
12. These values are significantly lower than the 18 to 87 percent values reported for female *B. germanica* [W. D. Valovage and M. A. Brooks, *Ann. Entomol. Soc. Am.* **72**, 687 (1979)] and the 8 to 31 percent reported for various species maintained in the laboratory [D. E. Mullins and D. G. Cochran, *Comp. Biochem. Physiol.* **53A**, 393 (1976)]. C. J. Potrikus and J. A. Breznak [*Insect Biochem.* **10**, 19 (1980)] reported that freshly collected termites contained approximately 2 percent uric acid; the amount increased to 45 percent for those in captivity, indicating that levels of uric acid might generally be higher in captive cockroaches as well.
13. The average dry weight of uricose glands in a natural population was 17.6 ± 1.2 mg ($N = 45$), which, if one assumes a urate content of 4.3 μ*M* per milligram of dry gland tissue as reported for *B. germanica* and *Nyctibora lutzi* [D. E. Mullins, *Comp. Biochem. Physiol.* **62A**, 699 (1979)], corresponds to 75.7 μ*M* of uric acid. We did not determine the urate content of *Xestoblatta* uricose glands.
14. W. J. Bell and M. Bohm, *Biol. Rev. Cambridge Philos. Soc.* **50**, 373 (1975).
15. D. G. Cochran, *Entomol. Exp. Appl.* **26**, 259 (1979).
16. M. H. Haydak, *Ann. Entomol. Soc. Am.* **46**, 547 (1953). D. E. Mullins and D. G. Cochran [*Comp. Biochem. Physiol.* **44B**, 549 (1973)] reported that mutagenic and carcinogenic tryptophan metabolites increase as dietary nitrogen increases. They

suggest that the quinoline compounds contribute to the increased mortality of *P. americana* on high-protein diets.
17. Other species of cockroaches copulate for about 20 to 120 minutes. G. A. Parker [*Biol. Rev. Cambridge Philos. Soc.* **45**, 525 (1970)] suggests that long mating sequences may be a form of mate guarding (and paternity assurance) whereby the female is unavailable to other males when she is most receptive.
18. D. E. Mullins and D. G. Cochran, *Comp. Biochem. Physiol.* **50A**, 501 (1975).
19. M. A. Brooks and K. Richards, *J. Invert. Pathol.* **8**, 150 (1966).
20. We thank Dr. Gabriel Macaya of the Universidad de Costa Rica for allowing us access to a scintillation counter and other equipment, and the Organization for Tropical Studies for logistic support. We gratefully acknowledge K. B. Armitage, D. G. Cochran, R. Jander, C. B. Keil, H. B. Lillywhite, C. D. Michener, D. E. Mullins, and R. Thornhill for critical review of the manuscript. This work was supported in part by NSF grants BNS-8006284 to W.J.B. and DEB-8007556 to C.S. and a Sigma Xi Grant-in-Aid of Research to C.S.
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Serial Position Curve in Rats: Role of the Dorsal Hippocampus

Abstract. *In an eight-arm radial maze, normal rats demonstrated good immediate retention for the order of first items (primacy component of serial position curve) and last items (recency component of serial position curve) of an eight-item (arm) list. In contrast, rats with dorsal hippocampal lesions displayed, on an immediate retention test, disruption of the primacy but not the recency component of the serial position curve. Furthermore, imposing a 10-minute delay before the retention test impaired all components of the serial position curve. These results support correspondence in mnemonic function of the hippocampus in animals and humans.*

The critical role of the hippocampus in the mediation of normal memory processes has been highlighted by the observation that in human patients bilateral damage to the medial temporal lobe, including the hippocampus, produces an extensive and durable amnesia for new information. The patients characteristically tend to forget daily events, have a relatively intact short-term memory (STM), but a deficient long-term memory (LTM) for specific events. Especially relevant to our experiment are the observations that amnesic patients with presumed hippocampal damage display (i) poor memory on an immediate test for the first items (primacy) of a list but excellent memory for the last items (recency) of the list, (ii) poor memory for all items of the list at a delayed test (*1*), and (iii) no apparent loss for general information relating to the rules for performing a particular task as long as specific information is available in STM (*2*).

We have observed in rats with hippocampal damage a pattern of memory deficits that parallels the human amnesic syndrome. In contrast to normal rats, who have good immediate memory for the order of presentation of the first and last items of a list of eight items (arms in a maze) and good memory only for the first, but not the last items, of the list at delayed retention tests, rats with dorsal hippocampal lesions have good immediate memory for the last, but not the first, items of the list, and have no memory for any of the items when retention tests are delayed. These data support the notion of correspondence in mnemonic function of the hippocampus in rats and humans and Iversen's hypothesis (*3*) that the correspondence was not previously observed because functionally equivalent tasks were not used. These data argue against the ideas that (i) the function of hippocampus is different for animals and humans, (ii) the amnesic syndrome produced by medial temporal lobe lesions is not due to hippocampal damage but rather is a function of damage to the temporal stem containing input and output pathways of temporal cortex and amygdala (*4*), and (iii) the amnesic syndrome is due not only to hippocampal damage but due to a combination of hippocampal plus amygdaloid damage (*5*).

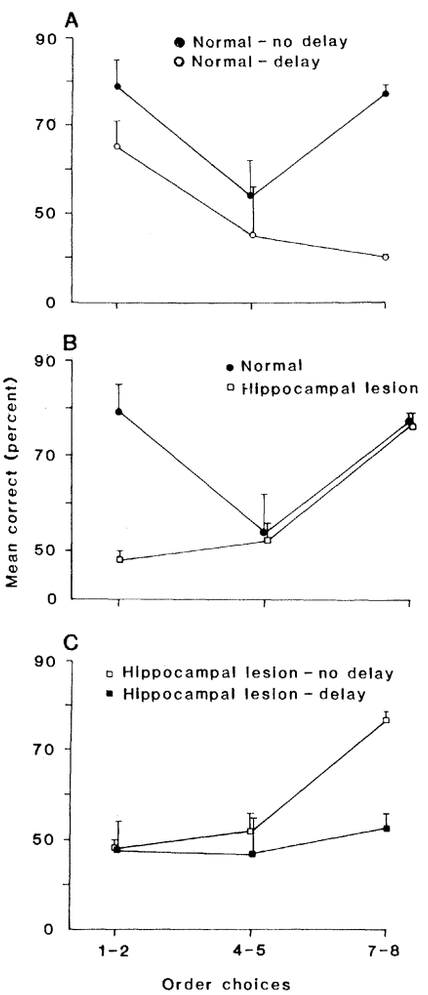

Fig. 1. (A) Serial position curve for normal subjects under no-delay (20-second) and delay (10-minute) conditions. (B) Serial position curve for normal and lesion states under an immediate retention test condition. (C) Serial position curve for subjects with hippocampal lesions under delay and no-delay conditions. I represents one standard error of the mean.

Four male Long-Evans rats 8 to 12 months old and weighing 360 to 480 g at the beginning of the experiment were studied. They were deprived of food to 80 percent of their free-feeding weight and allowed continuous access to water.

An elevated radial eight-arm maze similar to that described by Olton and Samuelson (*6*) was used with the addition of a set of clear Plexiglas doors that allowed the investigator to control access to any arm.

Animals were initially trained under the standard eight-arm procedure with all arms reinforced (*6*). Reinforcement consisted of small pieces of Froot Loops cereal. Once the animals were familiar with the apparatus and rapidly retrieved the food from each of the reinforced arms, they were switched to the serial list task. On each trial the animals were given access to the eight arms of the maze in a particular sequence and were tested 20 seconds later on their ability to discriminate which one of a given pair of arms was visited earlier in the sequence. The animals were first trained to a criterion of eight correct out of ten trials on a choice between the first and seventh arm in the sequence. This criterion was reached between 17 and 27 trials. After reaching criterion, each animal received at a 20-second delay on a random basis a choice (one test only) of either the first and second (1-2), fourth and fifth (4-5), or seventh and eighth (7-8) arms in the sequence. After 16 familiarization trials, each animal randomly received 12 trials for each 1-2, 4-5, and 7-8 position. All four rats displayed serial position effects, that is, prominent retention [better than chance (50 percent) performance] for 1-2 and 7-8 choice, but no retention (chance performance) for 4-5 choice (Fig. 1A). The same animals were then given 15 additional trials with five test trials for each 1-2, 4-5, and 7-8 choice but with the

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