larva spent about the next 2 days feeding on the roach on which the egg was laid. One larva in captivity fed continuously but had eaten only four roaches (*6*) 4 days after its mother opened its cell to begin provisioning (that is, at the beginning of what would have been the fifth day of provisioning, approximately 6½ days after the original oviposition). Thus, larvae were probably usually just starting to feed on provisioned roaches during the last days of provisioning when the females tended to rob.

Robbery of a cell, which involved one wasp discarding the contents of another wasp's cell and laying her own egg there, was seen only once, although the opportunity (one wasp ready to start a new cell, another with an open cell on the same nest) occurred 14 times. The female which committed this robbery had taken unusually long (7 or 8 days) to finish provisioning her previous cell.

By marking wasps as they first emerged from their cells, it was possible to show that the wasps on a given nest are probably often highly related. Five (perhaps six; one mark was equivocal) of eight females marked with model-airplane dope as they emerged returned to within 0.5 m of their mother nest 3 days after they emerged, and three (perhaps four) of them subsequently provisioned cells there. One of two males marked as they emerged also returned to his mother nest and subsequently mated with females emerging there (the other male was only poorly marked and may have returned but without his mark). Individual males patrolled the same nest each day for up to more than a month and chased other males from the site.

Thus, it is likely not only that a given wasp's nestmate is her sister, but also that the nestmate mated with the given one's brother. This mating system implies especially high relatedness with the offspring of nestmates. In other words, the altruistic behavior just described is performed to benefit individuals that are probably usually highly related, as predicted by Hamilton.

The pattern of robberies also conforms to Hamilton's predictions: robberies may usually occur only in situations of need because otherwise possible damage to the probably highly related offspring of nestmates would outweigh the benefits of a given wasp's offspring; and the fact that robberies are so restricted suggests that the cost to a wasp of permitting a robbery could be outweighed by the benefit to its own genes present in its neighbor's offspring.

The level of sociality exhibited by *T. cameronii* is very low, with no signs of the division of labor associated with many insect societies (*7*). Probably as a result of highly viscous populations, however, these wasps have developed behavior which overcomes the tendency toward intraspecific parasitism which is associated with the first steps of evolution from solitary to group life, and they derive the benefits (periodic nest defense, ready-made cells, and at least occasional reserves of prey in times of need) that group living provides.

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References and Notes

1. E. O. Wilson, in *Insect Behavior*, P. T. Haskell, Ed. (Royal Entomological Society, London, 1966), p. 81.
2. R. W. Matthews, *Science* **160**, 787 (1968); *Psyche* **75**, 1, 23 (1968).
3. The general biology of *T. cameronii*, with more detailed descriptions of most of the characteristics mentioned here, is in preparation. This study was conducted near Cali, Colombia (4°N latitude); the species occurs in Central America and northern South America.
4. W. D. Hamilton, *J. Theor. Biol.* **7**, 1, 17 (1964).
5. The average number of days spent provisioning, measured to the nearest half day, was 3.3 days (31 observations), range 1.5 to 5.0, median and mode 4.
6. The number of roaches consumed depended on their sizes. This larva ate one small and three medium-sized roaches.
7. By some criteria, such as those of C. D. Michener [*Annu. Rev. Entomol.* **14**, 299 (1969)] or E. O. Wilson [*The Insect Societies* (Harvard Univ. Press, Cambridge, 1971)], this species should be considered communal rather than truly social.
8. Supported by a grant from the Comité de Investigaciones, Universidad del Valle. I thank Dr. H. E. Evans for identifying the wasps and Dr. M. J. W. Eberhard and C. Garcia for stimulating discussions.

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Evolution of DNA Base Compositions in Microorganisms

Singer and Ames (*1*) proposed that ultraviolet light exerts a selective pressure for high percentages of guanine (G) plus cytosine (C) in the DNA (G + C content) of bacteria exposed to sunlight. They gave several examples of bacteria having both high G + C contents and what they considered to be a large amount of exposure to sunlight (organisms that form aerial conidia or fruiting bodies produce carotenoids to protect against photooxidation, or have a habitat near the surface of water). They also suggested as the most likely explanation for low G + C contents in bacteria some weaker selective pressures that are overwhelmed when the organism occupies a niche with high ultraviolet exposure. As possible weaker selective pressures they mentioned ionizing radiation and the natural occurrence of some alkylating chemicals. In support of this idea they gave several examples of obligate anaerobes and internal parasites all of which have low G + C contents. They noted only two examples (*Cytophaga* and *Saprospira*) that were difficult to explain by their theory.

Other bacteria may also be exceptions (Table 1). Bacteria which are well-adapted parasites of man and animals, according to the theory, are expected to have low G + C contents. The parasitic bacteria listed in Table 1 grow best at 37°C; in addition most of these bacteria are fastidious, and many are strict anaerobes. Generally, they cannot survive for very long outside their hosts, and the number of these bacteria which are exposed to sunlight must be very small. Some bacteria from aquatic environments also seem to be exceptions. One could not expect to find bacteria with a high G + C content in deep sea sediments. Some strictly anaerobic and nonphotosynthetic bacteria (*Desulfovibrio* and some *Spirochaeta*) are presumably not exposed to ultraviolet and these also have high G + C contents. In contrast, many pigmented and strictly aerobic bacteria, which are generally found near the surface of the water, have low G + C contents. It seems that most true marine bacteria, except for some micrococci, characteristically have lower G + C contents than their terrestrial counterparts. This is noteworthy, as a high proportion of marine bacteria occur in the zone of water exposed to sunlight ultraviolet.

An evaluation of the degree to which terrestrial bacteria are exposed seems more difficult. Singer and Ames judged members of the genus *Rhizobium*, 63 percent (G + C content is given as a percentage after the genus), to have a high exposure to sunlight. These organisms are adapted to grow on the roots of legumes where they form nodules. These and many other bacteria

(*Agrobacterium*, 62 percent; *Azotobacter*, 65 percent; *Azotomonas*, 61 percent) are typically soil organisms (*2*), but that does not necessarily mean that a great proportion of these bacteria are extensively exposed to sunlight. If exposure to ultraviolet of only a small part of the cell population of a given genus results in a selection of organisms with high G + C content, it would mean that ultraviolet is a much stronger selective agent than the pressures tending to lower the G + C content. Another organism, *Sporocytophaga myxococcoides*, which is a pigmented, strict aerobe and which forms microcysts (without fruiting bodies) might be expected to have a high G + C content. However, its base composition is 36 percent G + C.

Singer and Ames did not include in their study eucaryotic microorganisms because of the suggested screening of ultraviolet by their cell mass and pigmentation. However, these organisms also have a broad distribution of G + C contents (Fig. 1). The distribution of G + C contents in protozoa (22 to 65 percent), in fungi (27 to 70 percent), and in algae (36 to 68 percent) all ap-

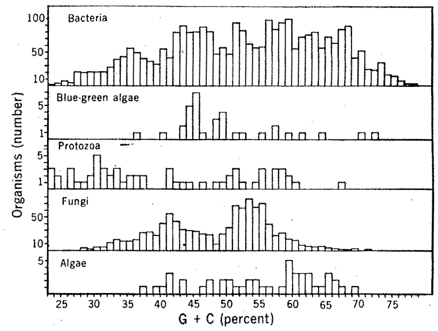

Fig. 1. Distribution of G + C contents in various groups of organisms (*2*). Bacteria including mycoplasmas (2762 strains), blue-green algae (34 strains), protozoa including slime molds (61 strains), fungi (989 strains), and algae (47 strains).

proach that found in bacteria. Many organisms within these groups occupy the same habitat but have very different G + C contents (*2*). Examples are protozoa in an aquatic environment (*Paramecium*, 30 percent; *Amoeba*, 66 percent), ubiquitous oceanic yeasts (*Candida diddensii*, 38 percent; *Rhodotorula rubra*, 63 percent) and freshwater algae (*Spirogyra*, 39 percent; *Chlamydomonas*, 64 percent). In procaryotic algae there are also examples of microorganisms with contrasting G + C contents in the same environment (*Gleocapsa alpicola*, 35 percent; and *Coccochloris peniocystis*, 71 percent).

Another consideration is the possible relation between thermophily and high G + C content. We have explored this possibility, but the available data (*3*) do not support such a correlation.

In view of the above we do not feel that the possible selective advantage presently envisaged can account for the distribution of G + C contents in unicellular organisms.

One of the predictions of the proposed major significance of the thymine dimers (after allowing for repair) is a correlation between high G + C content and resistance to ultraviolet. However, even under laboratory conditions the evidence from the published data on such a correlation seems doubtful (*4*).

In our opinion a critical evaluation of all published G + C values for microorganisms indicates that, apart from the selection away from extreme values, the distributions are largely random. One of the reservations to such a general statement is the conservation of certain DNA sequences (for example, the cistrons coding for ribosomes). The mechanism responsible for the observed distributions might be the low frequency of mistakes of the replication and repair systems. These error mechanisms could, even under stable conditions, be directional and slowly shift the G + C content. However, different mutation rates are presumably selected under natural conditions, with high mutation rates at an advantage when a unicellular organism is adapting to a new environment. Mutant phages and bacteria with high error frequency have been isolated. One of the bacterial mutator genes, *mut T*, causes a 1000-fold elevation of the mutation frequency (*5*). This mutator gene confers a selective advantage under some laboratory conditions (*6*); it also raises the G + C content (*7*). Another mutator gene may lower the G + C content (*8*). Much of the divergence of base composition in unicellular organisms may arise by such mutator gene action under conditions of rapid evolutionary change.

The existence of a random distribution of DNA base compositions is supported by examples of bacteria within the same habitat which have widely different G + C contents and which are thought to be phylogenetically related by conventional taxonomy. Such examples are (*2*): *Bordetella*, 68 percent;

Table 1. DNA base composition of different bacteria. The number of strains is given in brackets.

Genus	Species	G + C (%)
	*Human and animal parasites**	
Bordetella	*bronchiseptica* [1], *pertussis* [2]	68–70 (*9*)
Brucella	*abortus* [1], *melitensis* [1], *neotomae* [1], *ovis* [1], *suis* [1]	57–58 (*10*)
Neisseria	*gonorrhoeae* [1], *meningitidis* [2]	50–51 (*11, 12*)
Actinomyces	*bovis* [8]	68–76 (*13*)
Actinobacterium	*israeli* [12], *meyeri* [11], *abcessum* [7]	60–71 (*13, 14*)
Fusobacterium	*polymorphum* [1]	59 (*12*)
Bifidobacterium	*bifidum* [11], other species [18]	57–64 (*14, 15*)
Corynebacterium	*avidum* [1], *anaerobium* [1], *diphtheroides* [1], *lymphophilus* [1], 11 other species	52–58 (*14–16*)
Klebsiella	*pneumoniae* [27], *rhinoscleromatis* [6]	54–63 (*17, 18*)
Actinobacillus	*mallei* [2]	67 (*19*)
	Marine and freshwater bacteria	
Pseudomonas, Aeromonas, and unclassified bacteria	*Ps. bathycetes* [22] and other species [8]	56–59 (*20*)
Desulfovibrio	*desulfuricans* [44]	44–65, most about 55–60 (*18, 21*)
Spirochaeta	*stenostrepta* [1], *zuelzerae* [1]	55–60 (*22*)
Microscilla	7 species [20]	32–45 (*23*)
Flexibacter	12 species [21]	30–47 (*23*)
Pseudomonas	*piscicida* [20]	44–45 (*24*)
Micrococcus	5 species [9]	57–73 (*25*)
	eucinetus [1], 3 species [3],	40–44 (*25*)
	euryhalis [1], *halodurans* [1]	32–34 (*25*)
Flavobacterium	4 species [4]	36–41 (*26*)
Vibrio	*Vibrio* isolates [14]	39–48 (*27*)
Aeromonas	*Aeromonas* isolates [10]	39–42 (*28*)
Pseudomonas	*Pseudomonas* isolates [13]	41–49 (*28*)
Leucotrix	*mucor* [11]	47–50 (*29*)
Beggiatoa	*leptomitiformis* [1]	37 (*23*)
Vitreoscilla	1 species [1]	44 (*23*)

* All examples presented have an optimum temperature of 37°C and are nonpigmented and nonsporulating.

Haemophilus, 38 percent; the thermophilic actinomycetes, 44 to 77 percent; *Proteus vulgaris*, 39 percent; *P. morganii*, 50 percent; mycoplasmas, 23 to 39 percent; *Neisseria catarrhalis*, 41 percent; *N. meningitidis*, 51 percent; and variations within genera *Bacillus*, 33 to 53 percent; *Clostridium*, 27 to 48 percent; *Halobacterium*, 55 to 68 percent; *Lactobacillus*, 34 to 53 percent; and marine *Micrococcus*, 57 to 73 percent.

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References and Notes

1. C. E. Singer and B. N. Ames, *Science* **170**, 822 (1970).
2. A complete list of references on G + C contents in microorganisms is available from the authors on request.
3. G. Darland, T. D. Brock, W. Samsonoff, S. F. Conti, *Science* **170**, 1416 (1970); J. Stenesh, B. A. Roe, T. L. Snyder, *Biochim. Biophys. Acta* **161**, 442 (1968); T. D. Brock and H. Freeze, *J. Bacteriol.* **98**, 289 (1969); R. Craveri, L. R. Hill, P. L. Manachini, L. G. Silvestri, *J. Gen. Microbiol.* **41**, 335 (1965); H. Prauser, *Spisy Prirodoved. Fak. Univ. J. E. Purkyne Brne Ser. K* **38**, 268 (1966).
4. M. R. Zelle and A. Hollaender, *Radiat. Biol.* **11**, 365 (1955); R. H. Haynes, in *Physical Processes in Radiation Biology. International Symposium on Physical Processes in Radiation Biology, 1963* (Academic Press, New York, 1966), p. 51.
5. H. P. Treffers, V. Spinelli, N. O. Belser, *Proc. Nat. Acad. Sci. U.S.* **40**, 1064 (1954).
6. T. C. Gibson, M. L. Scheppe, E. C. Cox, *Science* **169**, 686 (1970).
7. E. C. Cox and C. Yanofsky, *Proc. Nat. Acad. Sci. U.S.* **58**, 1895 (1967).
8. E. B. Freese and E. Freese, *ibid.* **57**, 650 (1967).
9. J. De Ley, *Antonie van Leeuwenhoek J. Microbiol. Serol.* **34**, 109 (1968); M. F. Bacon, W. G. Overend, P. A. Lloyd, A. R. Peacocke, *Arch. Biochem. Biophys.* **118**, 352 (1967).
10. B. H. Hoyer and N. B. McCullough, *J. Bacteriol.* **95**, 444 (1968).
11. B. W. Catlin and L. S. Cunningham, *J. Gen. Microbiol.* **26**, 303 (1961).
12. A. N. Belozersky and A. S. Spirin, in *The Nucleic Acids*, E. Chargaff and J. N. Davidson, Eds. (Academic Press, New York, 1960), vol. 3, p. 147.
13. L. Bouisset, J. Breuilland, G. Michel, G. Larrouy, *Ann. Inst. Pasteur* **115**, 1063 (1968).
14. M. Sebald, F. Gasser, H. Werner, *ibid.* **109**, 251 (1965).
15. F. Gasser and M. Mandel, *J. Bacteriol.* **96**, 580 (1968).
16. L. Bouisset, J. Breuilland, G. Michel, *Ann. Inst. Pasteur* **104**, 756 (1963).
17. M. Mandel and R. Rownd, in *Taxonomic Biochemistry and Serology*, C. A. Leone, Ed. (Ronald, New York, 1964), p. 585; M. P. Starr and M. Mandel, *J. Gen. Microbiol.* **56**, 113 (1969); J. N. Baptist, C. R. Shaw, M. Mandel, *J. Bacteriol.* **99**, 180 (1969).
18. C. A. Ouelette, R. H. Burris, P. W. Wilson, *Antonie van Leeuwenhoek J. Microbiol. Serol.* **35**, 275 (1969).
19. M. Rogul, J. J. Brendle, D. K. Haapala, A. D. Alexander, *J. Bacteriol.* **101**, 827 (1970).
20. M. A. Hogan and R. R. Colwell, *J. Appl. Bacteriol.* **32**, 103 (1969).
21. G. F. Saunders, L. L. Campbell, J. R. Postgate, *J. Bacteriol.* **87**, 1073 (1964); N. Sigal, J. C. Senez, J. L. Gall, M. Sebald, *ibid.* **85**, 1315 (1963).
22. E. Canale-Parola, Z. Udris, M. Mandel, *Arch. Microbiol.* **63**, 385 (1968).
23. M. Mandel and R. A. Lewin, *J. Gen. Microbiol.* **58**, 171 (1969).
24. M. Mandel, O. B. Weeks, R. R. Colwell, *J. Bacteriol.* **90**, 1492 (1965); A. J. Hansen, O. B. Weeks, R. R. Colwell, *ibid.* **89**, 752 (1965).
25. J. Boháček, M. Kocur, T. Martinec, *J. Appl. Bacteriol.* **31**, 215 (1968).
26. J. De Ley and J. van Muylem, *Antonie van Leeuwenhoek J. Microbiol. Serol.* **29**, 344 (1963).
27. R. V. Citarella and R. R. Colwell, *J. Bacteriol.* **104**, 434 (1970); R. R. Colwell, V. F. Adeyemo, H. H. Kirtland, *J. Appl. Bacteriol.* **31**, 323 (1968); R. R. Colwell and M. Mandel, *J. Bacteriol.* **88**, 1816 (1964).
28. E. Leifson and M. Mandel, *Int. J. Syst. Bacteriol.* **19**, 127 (1969).
29. T. D. Brock and M. Mandel, *J. Bacteriol.* **91**, 1659 (1966).
30. We thank N. O. Kjeldgaard and A. Stenderup for their critical review of the manuscript. J.F.A. is supported by a fellowship from the European Molecular Biology Organization.

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We have previously proposed (*1*) that bacterial species exposed to sunlight evolved high G + C contents to avoid thymine specific damage from the ultraviolet radiation in sunlight, and this could be one of the explanations for the wide variation of G + C ratios in bacteria. We presented evidence that there was a good correlation between the amount of sunlight to which bacterial "genera" were normally exposed and their G + C content. We also presented calculations on the amount of ultraviolet that bacteria were exposed to and its effect. Leth Bak *et al.* (*2*) take issue with us in that they find a number of exceptions to our generalization. They consider a fairly small number of individual species, whereas we considered "genera" so as to reduce the influence of minor fluctuations (due to misclassification, poorly understood habitats, and so forth) on individual species, and we considered all 73 "genera" whose G + C contents were known at that time. We still think that the overall correlation is striking and that some individual exceptions are to be expected, in part because of the difficulties in classification and the uncertainties of determining the normal habitats of bacteria in nature.

The alternate explanation of Leth Bak *et al.* that the variation in G + C contents is random (and therefore not otherwise explicable) was one that we discussed (*1*, reference 26), and we pointed out that a *truly random* distribution of G + C contents would leave virtually all bacteria within 1 percent of the mean. This implies that G + C content must reflect underlying, evolutionary forces. We still hold that ultraviolet damage is a tremendous force in the life of microorganisms, that organisms with a high G + C content would be more resistant to damage by ultraviolet, and that this seems the most likely evolutionary force to explain the variation in G + C ratios. Further work on the normal life habitats and evolution of microorganisms will presumably clarify this question.

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References

1. C. E. Singer and B. N. Ames, *Science* **170**, 882 (1970).
2. A. Leth Bak, J. F. Atkins, S. A. Meyer, *ibid.* **175**, 1391 (1972).

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Bohr Atom: A Remark on the Early History

In his excellent book (*1*) *The Conceptual Development of Quantum Mechanics*, Max Jammer discusses a paper (*2*) by my teacher, F. Hasenöhrl, and one of mine (*3*), based on it. He says (p. 75):

> In March 1912 Herzfeld proposed a modification of Thomson's model by assuming circular electronic orbits and a non-uniform charge density of the positive sphere and derived from these assumptions the Balmer series by a quantization of energy in accordance with a rule formulated by Hasenöhrl as generalization of Planck's prescription for the quantization of the harmonic oscillator. But all these and similar calculations . . . lost their validity with the abandonment of the Thomson model on which they are based.

While this description is historically correct, the last sentence misses, in my opinion, an essential point. Hasenöhrl used no model whatever, while the model I used is sufficiently general.

The matter might seem too trivial to discuss further, but a point which is quite important in my opinion and has not been emphasized elsewhere is closely connected with it. Since I am the only survivor of the three involved—Bohr, Hasenöhrl, and myself—I may be permitted to dwell on the matter; I