# Life in Ice-Covered Oceans

**ARTICLE** *in* SCIENCE · JULY 1999

**3 AUTHORS**, INCLUDING:

Kenneth Nealson
University of Southern California

Life in Ice-Covered Oceans
Author(s): Eric J. Gaidos, Kenneth H. Nealson, Joseph L. Kirschvink
Source: *Science*, New Series, Vol. 284, No. 5420 (Jun. 4, 1999), pp. 1631-1633
Published by: American Association for the Advancement of Science
Stable URL: http://www.jstor.org/stable/2898637
Accessed: 11/11/2009 16:01

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 service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. 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

**PERSPECTIVES: BIOGEOCHEMISTRY**

# Life in Ice-Covered Oceans

**Eric J. Gaidos, Kenneth H. Nealson, Joseph L. Kirschvink**

Recent evidence for salt water oceans beneath the ice crusts of Europa and Callisto (*1*, *2*) has bolstered speculation that these satellites of Jupiter may harbor life (*3*, *4*). Attention has focused on Europa. The geology and young age of its surface (*5*, *6*) and the predicted heat flow from radiogenic decay and tidal dissipation (*7*, *8*) suggest a geologically active interior and liquid water at shallower depths. To assess the plausibility of life on Europa and suggest which kinds of organisms are most likely to inhabit this ocean, we must look at the fundamental requirements for life on Earth.

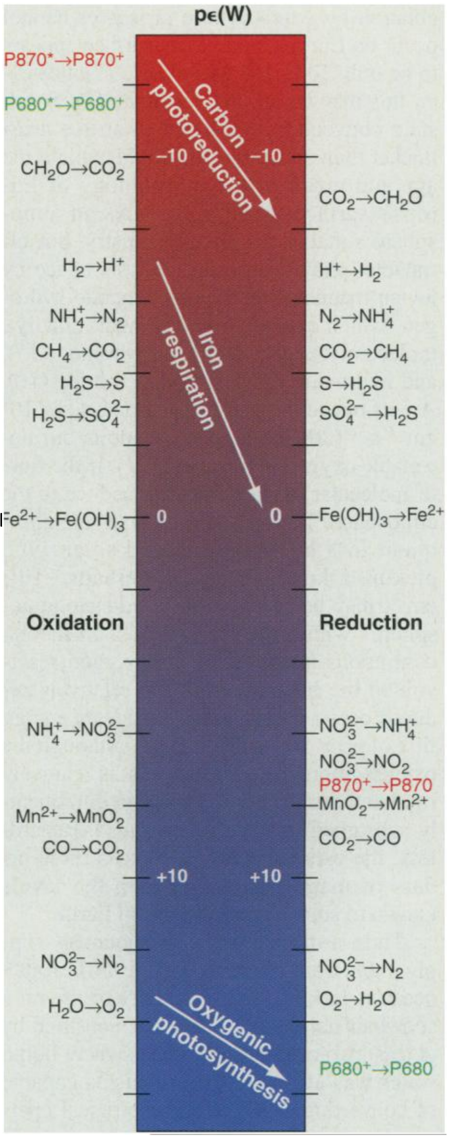
In addition to liquid water and a supply of suitable chemical elements, organisms on Earth require a source of energy for metabolism, growth, maintenance, and reproduction. This energy is derived primarily from sunlight through photosynthesis (in certain bacteria and the bacterially derived chloroplasts of plants) or photorespiration (in archaea living in salty environments); a very small proportion is derived from geothermally driven chemical disequilibria. The chemical products of this activity span a range of oxidation potentials that drive a cascade of intermediate oxidation-reduction (redox) reaction pairs (see the figure). Organisms on Earth exploit these thermodynamically favored reactions as energy sources, and combinations of oxidants and reductants support various metabolic life-styles. Before the evolution of photosynthesis, organisms could not use sunlight directly, and life on Earth depended on abiotic sources of chemical energy in the form of disequilibrium concentrations of redox reactants driven by hydrothermal activity, solar ultraviolet radiation, electrical discharges, and impacts (*9*). All these redox pairs are depleted by abiotic reactions and biological activity, and without an external energy source such as sunlight (or internal geothermal energy), chemical equilibration will ultimately extinguish all life. This thermodynamic reality imposes severe constraints on any biota on Europa that is based on chemical energy.

If an ocean exists on Europa, it is physically and chemically isolated by an ice crust 10 to 100 km in thickness (*1*). We have to go back far into Earth's climatic history to find a possible analogy for this situation. Kilometer-thick ice may have entombed Earth's oceans during "snowball" episodes of global glaciation, which are believed to have persisted for 5 to 50 million years (My) during the Proterozoic (about 2500 to 570 My before present) until the buildup of atmospheric $CO_2$ from volcanoes created a greenhouse effect strong enough to melt the ice (*10*).

Without photosynthesis or contact with an oxidizing atmosphere, an isolated subsurface ocean will approach chemical equilibrium and annihilate any ecosystems dependent on redox gradients unless there is a substantial alternative (for example, geothermal) energy source. The terrestrial ocean circulates through the hydrothermal systems of mid-ocean spreading ridges in ~10 My (*11*) and would equilibrate with the chemistry of the basaltic magmas that make up the ocean floor in these regions on that (geologically short) time scale. Biological activity would only accelerate the process of equilibration, ensuring its own destruction by consuming the limited supply of oxidants. Hydrothermal alteration and weathering would likewise drive the equilibration of oceanic and silicate crust chemistry. Thermodynamics-driven extinctions would ensue on both Europa and a "snowball" Earth. Under Europas permanent ice crust they may have been terminal.

Hydrothermal vents have been cited as potential analogs to life on Europa, because they do not receive sunlight and appear to be isolated from other ecosystems. The vent ecosystems, however, depend almost exclusively on oxidants ($SO_4^{2-}$, $O_2$, and $CO_2$) dissolved and transported from the surface to the deep ocean (*12*). More than 99% of the energy available to known vent biotas is from sulfate reduction, sulfur oxidation, and aerobic metabolism (*13*). Without oxidants from the surface ocean, organisms would have to rely on low-energy methanogenesis and elemental sulfur reduction. The flux of available energy from these reactions in the most active vent fields is only ~$5 \times 10^{-3}$ ergs $cm^{-2}$ $s^{-1}$ (*14*). For comparison, the primary production in the upper ocean (*15*) is equivalent to a biological energy flux of ~10 ergs $cm^{-2}$ $s^{-1}$, and this is only 0.01% of the total energy available in sunlight. It is unclear that such low energy fluxes could support extensive life on the sea floor.

Life may persist, however, if a flux of oxidants into the subsurface ocean can be maintained. To understand how this might happen, we must compare the geology and atmosphere of Europa with that of a "snowball" Earth.



**The thermodynamics of life.** Organisms harvest energy by coupling energetically favorable pairs of oxidation and reduction half-reactions. Reactions of common inorganic substrates are plotted according to their redox potential *p*ε at 1 atm, pH = 7, and 25°C (*43*). $[Fe^{2+}]$ is taken to be $10^{-5}$ M. Water and protons are not shown in the equations. Only redox reaction pairs with a negative net redox potential can provide energy. The primary donors of photosynthetic Photosystem I (P870) and II (P680) are strong reducers in their excited state and are used to fix carbon. In the oxidative (rest) state, only P680 is capable of oxidizing water, producing oxygen.

Residual disequilibrium would persist in an ice-covered ocean to the extent that turnover in the ice crust can introduce oxidants into the ocean. Diffusion of gases through low-temperature ice is essentially zero (*16*). On a "snowball" Earth, turnover of the ice sheet and transport of oxygen to the ocean could occur through sublimation and thermally driven transport of water vapor from the equator to the poles or through

---

E. J. Gaidos and J. L. Kirschvink are in the Geology and Planetary Sciences Division, California Institute of Technology, Pasadena, CA 91125, USA. E-mail: gaidos@gps.caltech.edu. K. H. Nealson is in the Center for Great Lake Studies, University of Wisconsin–Milwaukee, Milwaukee, WI 53204–2944, USA.

ablation by winds. These processes cannot occur on Europa, and yet its surface appears to be only 10 to 100 My old (*1*, *17*), however, this may be an underestimate (*8*). Solid-state convection, predicted in an ice crust thicker than about 10 km, would explain the age and much of the morphology of Europa's surface (*5*). Europa lacks an atmosphere suitable for photochemistry, but ultraviolet photolysis and radiolysis of ice by jovian magnetospheric ions generate hydrogen (which escapes from the weak gravity), molecular oxygen, hydrogen peroxide (*18*), and hydroxide radicals within the ice (*19*). An estimated oxygen production rate of $10^9$ $cm^{-2}$ $s^{-1}$ (*20*) maintains a tenuous but detectable oxygen atmosphere (*21*). If the flow of molecular oxygen from surface ice to the atmosphere is much slower than its subsequent loss by sputtering and solar wind pickup, a larger reservoir, perhaps $\sim 10^{22}$ $cm^{-2}$, may be stored in a "solid-state atmosphere" within the ice (*19*, *22*). In theory, continuous transport of this oxygen reservoir to the interface with the relatively reduced ocean waters could provide an energy flux of $\sim 3 \times 10^{-4}$ ergs $cm^{-2}$ $s^{-1}$, although the oxygen-impregnated outer crust is relatively rigid and brittle and may only be infrequently subsumed into the interior (*23*). Regardless, the estimated energy flux is three orders of magnitude lower than the levels known to support ecosystems on Earth.

Thus, a mechanism to continuously supply significant oxidants for life in Europa's ocean is lacking. The continuity of life on a snowball Earth would have been ensured by at least two near-surface niches where liquid water was available for organisms capable of converting sunlight into biological energy. Water with little or no ice cover would be found in continental hot springs like the Yellowstone and Mammoth calderas or over shallow rifting zones such as Iceland. Also, liquid water inclusions form around sediment particles heated by the sun at shallow depths in sublimating ice (*24*), and bacteria capable of carrying out photosynthesis at the low light levels found beneath several meters of ice (*3*, *25*) would support a food chain in these near-surface environments.

In contrast, the surface of Europa is highly unlikely to support any type of life requiring liquid water. Surface temperatures are less than 128 K (*26*), and the water melting point is reached only at depths exceeding ~20 km, whereas sunlight penetrates to depths of tens of meters only (*27*). Cracks in the crust are also unlikely to allow sunlight to reach an interior ocean for even brief periods (*28*), contrary to earlier suggestions (*3*). Large impacts may puncture the ice shell (*29*), but these events are likely to be transient and rare throughout most of the satellite's history. Transient brines could occur at shallow depths over diapiric plumes of warm ice (*5*, *30*), but individual diapirs form on time scales of $<10^5$ years (*31*) and any brines freeze by conductive cooling in $\sim 10^3$ years, brief periods relative to the turnover time of the ice crust. It seems unlikely that such bodies of water, isolated and subsequently frozen for $10^7$ years, could perpetuate a global biosphere.

We are left with geochemical reactions such as methanogenesis and elemental sulfur reduction as the main driving forces for potential life on Europa. These reactions have been proposed as the basis for metabolism on the primitive Earth (*32*), particularly for ecosystems in subsurface refugia protected from the sterilizing effects of large impacts (*33*, *34*), and as an energy source for life on other solar system bodies (*14*, *35*). They may also be the last resort for life in ice-covered oceans. The energy source is a "geothermocouple" created when the direction of a redox reaction at high temperature is opposite to that at low temperature but the latter is kinetically inhibited, creating disequilibrium (*35*). Biological catalysis of the low-temperature reaction then extracts useful energy from the geothermal gradient. Energy will be available as long as the temperature differential persists and there is a flux of reactants (typically compounds of carbon, sulfur, hydrogen, and iron) through the high- and low-temperature regimes.

The C, S, and H compounds are replenished over long periods of time from gases released by the crust ("outgassing") or by hydrothermal circulation. In contrast, iron, involved in many geochemical reactions, requires replenishment of chemically active rock from the mantle by volcanism or tectonics. Otherwise, the iron in the reaction zone will be completely oxidized, geochemical reactions will halt, and any dependent biology will be extinguished. Hydrothermal alteration at terrestrial mid-ocean ridges would proceed to completion in less than $10^3$ years in the absence of new crust continuously created by sea-floor spreading.

On a snowball Earth, plate tectonics, volcanism, and submarine hydrothermal activity would continue unabated. The geodynamics of Europa are completely unknown. It has been suggested that the satellite may have a metal core and silicate mantle (*36*) with an estimated heat flow from the metal silicate interior 10 to 30% of that of Earth (*8*) and comparable to that of Mars (*37*), which has experienced substantial extrusive volcanism in the past (*38*, *39*). It is plausible, but not established, that episodic volcanism and hydrothermal activity may also occur at an ocean-mantle boundary on Europa.

Hydrothermal alteration of Earth's upper mantle and crust oxidizes iron to produce the reductant hydrogen. Outgassed carbon equilibrates under conditions that produce the oxidant $CO_2$. Subducted carbonates are also outgassed as $CO_2$. Biology can then exploit the energy made available by the methanogenesis reaction $CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$. The hydrothermal production of hydrogen would cease once oxdiation of the crust was complete, but plate tectonics has effectively "buffered" the oxidation state of the crust with that of the mantle (*40*). On Europa, methanogenesis may not be a viable energy source even if volcanic and tectonic activity are present, because its mantle, without the subduction of oxidants, could be more reducing than Earth's crust and the 1- to 2-kbar pressure at the water-silicate boundary will shift the gaseous $CO_2$-$CH_4$ equilibrium (at a given oxygen fugacity) to higher temperatures. Hydrothermal activity will then produce abundant hydrogen, but carbon will outgas as methane, rather than as $CO_2$. Likewise, sulfur would appear as sulfide rather than as oxidants such as elemental sulfur or sulfur dioxide (*41*). It thus appears unlikely that either methanogenesis or elemental sulfur reduction would be able to support life on Europa.

The above considerations illustrate that nearly all metabolic life-styles on the present Earth would be denied to organisms inhabiting an ice-covered ocean on Europa because soluble oxidants will not be produced or transported into the water column. Geochemical energy could power a relatively feeble ecology but requires volcanic resurfacing or plate tectonics. Even if Europa's interior is geologically active, energy-generating reactions such as methanogenesis and sulfur reduction used by terrestrial organisms will not be available to hypothetical life forms because carbon and sulfur will be outgassed as reduced rather than oxidized species.

This severe paucity of oxidants cautions against expectations that diverse, thriving life will be found in a European ocean. The only plausible oxidants may be oxidized metals such as ferric iron. The low-temperature reduction of $Fe_2O_3$ by hydrogen, methane, or (hydrogen) sulfide is thermodynamically favorable especially under local conditions of low $[Fe^{2+}]$ or acidic pH (*42*). These reactions might support a simple ecology within hydrothermally weathered rock percolated by ocean water with dissolved $H_2$, $CH_4$, and $H_2S$. Hydrogen-, methane-, and sulfur-oxidizing bacteria are ubiquitous on Earth (*43*), and two groups of mineral iron-reducing bacteria are known (*44*). Among the latter are bacteria that use hydrogen as a reductant. These organisms may metabolically resemble those that could function in a European biogeochemical cycle.

**References and Notes**

1. M. H. Carr *et al.*, *Nature* **391**, 363 (1998).
2. K. K. Khurana *et al.*, *ibid.* **395**, 777 (1998).
3. R. T. Reynolds, S. W. Squyres, D. S. Colburn, C. P. McKay, *Icarus* **56**, 246 (1983).
4. S. Mood, *Astronomy* **11**, 16 (1983); R. T. Reynolds, C. P. McKay, J. F. Kasting, *Adv. Space Res.* **7** (5), 125 (1987); C. S. Powell, *Sci. Am.* **276**, 28 (January 1997); F. J. Dyson, *Atl. Mon.* **280**, 71 (November 1997).
5. R. T. Pappalardo *et al.*, *Nature* **391**, 365 (1998).
6. R. Greeley *et al.*, *Icarus* **135**, 4 (1998).
7. P. M. Cassen, R. T. Reynolds, S. J. Peale, *Geophys. Res. Lett.* **6**, 731 (1979); M. N. Ross and G. Schubert, *Nature* **325**, 133 (1987); G. W. Ojakangas and D. J. Stevenson, *Icarus* **81**, 220 (1989).
8. S. W. Squyres *et al.*, *Nature* **301**, 225 (1983).
9. S. Chang, in *The Chemistry of Life's Origins*, J. M. Greenberg *et al.*, Eds. (Kluwer Academic, Boston, 1993), pp. 259–299; R. Navarro-Gonzalez, M. J. Molina, L. T. Molina, *Geophys. Res. Lett.* **25**, 3123 (1998).
10. J. L. Kirschvink, in *The Proterozoic Biosphere: A Multidisciplinary Study*, J. W. Schopf and C. Klein, Eds. (Cambridge Univ. Press, Cambridge, 1992), pp. 51–52; P. F. Hoffmann, A. J. Kaufman, G. P. Halverson, D. P. Schrag, *Science* **281**, 1342 (1998).
11. H. Elderfield and A. Schultz, *Annu. Rev. Earth Planet. Sci.* **24**, 191 (1996).
12. V. Tunnicliffe, *Oceanogr. Mar. Biol.* **29**, 319 (1991); R. A. Lutz and M. J. Kennish, *Rev. Geophys.* **31**, 211 (1993).
13. T. M. McCollom and E. L. Shock, *Geochim. Cosmochim. Acta* **61**, 4375 (1997).
14. B. M. Jakosky and E. L. Schock, *J. Geophys. Res.* **103**, 19359 (1998).
15. G. A. Knauer, in *Interactions of C, N, P, and S. Biogeochemical Cycles and Global Change*, R. Wollast, F. T. MacKenzie, L. Chou, Eds. (Springer-Verlag, New York, 1993), pp. 211–231.
16. P. Jean-Baptiste, *Earth Planet. Sci. Lett.* **158**, 81 (1998).
17. K. Zahnle, L. Dones, H. F. Levison, *Icarus* **136**, 202 (1998).
18. R. W. Carlson *et al.*, *Science* **283**, 2062 (1999).
19. R. E. Johnson and T. I. Quickenden, *J. Geophys. Res.* **102**, 10985 (1997).
20. W.-H. Ip, *Icarus* **120**, 317 (1996).
21. D. T. Hall *et al.*, *Nature* **373**, 677 (1995).
22. Y. L. Yung and M. T. Leu, paper presented at the American Astronomical Society Division of Planetary Science Meeting 28, Tucson, AZ, 1996; M. L. Delitsky and A. L. Lane, *J. Geophys. Res.* **102**, 16385 (1997); R. E. Johnson and W. A. Jesser, *Astrophys. J.* **480**, L79 (1997).
23. N. A. Spaun *et al.*, *Geophys. Res. Lett.* **25**, 4277 (1998).
24. J. C. Priscu *et al.*, *Science* **280**, 2095 (1998).
25. J. Overmann, H. Cypiowka, N. Pfennig, *Limnol. Oceanogr.* **370**, 150 (1992).
26. G. S. Orton *et al.*, *Science* **274**, 389 (1996).
27. P. V. Hobbs, *Ice Physics* (Clarendon, Oxford, 1974).
28. G. D. Crawford and D. J. Stevenson, *Icarus* **73**, 66 (1988).
29. J. M. Moore *et al.*, *ibid.* **135**, 127 (1998).
30. R. Sullivan *et al.*, *Nature* **391**, 371 (1998).
31. J. A. Rathbun *et al.*, *Geophys. Res. Lett.* **25**, 4157 (1998).
32. E. L. Shock, in *Evolution of Hydrothermal Ecosystems on Earth (and Mars)* (Wiley, Chichester, England, 1996), vol. 202, pp. 40–60.
33. K. A. Maher and J. D. Stevenson, *Nature* **331**, 612 (1988).
34. N. H. Sleep, K. J. Zahnle, J. F. Kasting, H. J. Morowitz, *ibid.* **342**, 139 (1989).
35. E. L. Shock, *J. Geophys. Res.* **102**, 23687 (1997).
36. J. D. Anderson *et al.*, *Science* **281**, 2019 (1998).
37. F. Sohl and T. Spohn, *J. Geophys. Res.* **102**, 1613 (1997).
38. R. Greeley and B. D. Schneid, *Science* **254**, 996 (1991).
39. H. Y. McSween, *Meteoritics* **29**, 757 (1994).
40. C. Ballhaus *et al.*, *Nature* **348**, 437 (1990).
41. Extrusion or outgassing of sulfide and subsequent oxidation on the surface could be responsible for the observed sulfates [T. McCord *et al.*, *Science* **280**, 1242 (1998)].
42. W. Stumm and J. J. Morgan, *Aquatic Chemistry* (Wiley, New York, ed. 2, 1981).
43. J. C. Murrell, *FEMS Microbiol. Rev.* **88**, 233 (1992); C. G. Friedrich, *Adv. Microb. Physiol.* **39**, 235 (1998).
44. T. J. DiChristina, R. G. Arnold, M. E. Lidstrom, M. R. Hoffmann, *Water Sci. Technol.* **20**, 69 (1988); D. R. Lovley and E. F. Phillips, *Appl. Environ. Microbiol.* **51**, 683 (1988); C. R. Myers and K. H. Nealson, *J. Bacteriol.* **172**, 6232 (1990).
45. We thank Y. Yung and E. Shock for useful discussions.

PERSPECTIVES: BEHAVIOR

# Selfish Sentinels

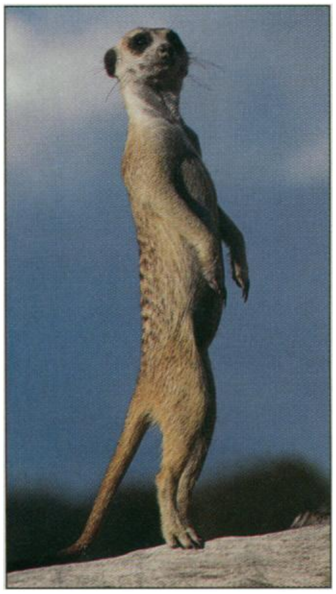
**Daniel T. Blumstein**

The selfless behavior of sentinels—the guards who take turns in keeping watch, putting themselves at risk for the benefit of others—has always been a human activity that people want to believe is found in other species too. In a variety of birds and mammals (*1*) that live in social groups, it is well documented that certain individuals act as guards while others forage for food and go about their daily routines. In some species, individuals trade-off sentinel duties in a coordinated fashion (*2*), perhaps to spread the danger evenly because guards are believed to be exposed to a greater risk of predation (*3*). What selection processes could explain the existence of such a potentially risky behavior in a large number of unrelated species? The popular view has been that sentinel behavior is influenced primarily by kin selection, that is, individuals tend to engage in behavior that benefits their relatives. But, on page 1640 of this issue, Clutton-Brock and colleagues present an elegant study in the African mongoose (*Suricata suricatta*) that dispels the myth of kinship and instead supports the opposing view that sentinel behavior is a selfish not selfless activity (*4*).

Enhanced online at www.sciencemag.org/cgi/content/full/284/5420/1633

The insight that individuals may enhance fitness by engaging in activities, such as coordinated sentinel behavior, that benefit their relatives has revolutionized the study of animal behavior in the past few decades (*5*). Reciprocal altruism (*6*), whereby individuals take turns in allocating time to sentinel duties, is also likely in highly social species in which individuals can easily recognize each other and therefore keep track of those shirking guard duty. Unfortunately, assumptions and presumptions about selfless sentinel behavior have led some to believe that it is more common and potentially more complex than it really is. More importantly, the assumed mechanisms, although theoretically convenient, may in fact not be true.

Recently, Bednekoff has questioned a variety of assumptions often made about the selfless behavior of sentinels (*1*). He developed a convincing model to explain how apparently coordinated guarding could emerge from individually selfish antipredator behavior. He first noted that there was no concrete evidence that sentinels were actually more likely to be killed while on guard than their less vigilant, foraging group mates. Turning this assumption around, Bednekoff pointed out that sentinels may detect and avoid approaching predators more readily than foraging animals. Thus, rather than being exposed to an increased risk of predation, sentinels might actually be safer than the rest of the group. Such an explanation could account for cases where individuals compete for sentinel positions (*7*). He also noted that sentinel behavior could be influenced by a sentinel's nutritional state. Hungry animals would be less likely to engage in sentinel behavior than their better-fed comrades. Based on these two assumptions, he concluded that complex sentinel behavior could take place in the absence of any kin-selected benefits.



**Attention!** Sentinel behavior among suricates (a type of mongoose), rather than being a selfless act that helps to save a sentinel's relatives, confers a benefit on the guards themselves. They are usually the first to detect predators and are closer than their foraging colleagues to burrows, down which they can readily escape.

Bednekoff's theoretical findings are at the forefront of contemporary behavioral ecological studies that seek to properly identify the role and scope of kin selection and to provide alternative mechanisms to explain the evolution of behaviors. In this case, sentinel behavior

---

The author is in the Departments of Biology and Psychology, Macquarie University, Sydney, NSW 2109, Australia. E-mail: dan@galliform.bhs.mq.edu.au