the Prisoner's Dilemma using a similar experimental setup (apart from the transparent food trays). Even when birds were trained to cooperate initially, they switched to sustained mutual defection. The reasons were unclear. Do nonhuman animals lack the capacity for reciprocal cooperation? Or was a failure to cooperate due to the unnatural conditions of the experiment?

Another explanation now appears more likely. In the new set of experiments, Stephens *et al.* (*2*) show that blue jays are indeed capable of sustained cooperation. The key is to recognize that, relative to rewards from defection, rewards from cooperation may be delayed. The effect of such a delay is to reduce the immediate value of any cooperative benefit from, say, B to only αB, where α depends inversely on the strength of temporal discounting, that is, on the strength of the preference for an immediate versus a delayed reward (*6*). This effect may be considerable; for example, as Stephens *et al.* (*2*) note, a delay of only a second may imply $\alpha = 0.5$. So a bird may prefer one seed now to two seeds in the very near future. Despite that, in studying cooperation, behavioral ecologists have largely assumed $\alpha = 1$.

Although in principle it isn't hard to see that temporal discounting can make the difference between sustained cooperation or defection, it is considerably more difficult to demonstrate this effect in practice. Yet this is precisely what Stephens *et al.* (*2*) have achieved: They found that birds care less about the immediacy of rewards if seeds accumulate in a transparent food tray for some time before being disbursed. Most birds then cooperate if their partner does so as well.

The study is timely because it forces behavioral ecologists not only to rethink the potential importance of temporal discounting, but also to address a number of other issues. For example, even when temporal discounting was high, some blue jays achieved significant levels of cooperation whereas others did not. Thus, there is apparent variability in the propensity of individuals of the same species to cooperate. The consequences may be important, just as intrinsic variation in fighting ability strongly affects the strategic stability of contest behavior in animals (*7*). Humans also vary in their propensity to cooperate (for example, between males and females, or between economists and noneconomists) (*8*). And how, precisely, do animals condition their behavior according to the behavior of another in order to achieve cooperation when discounting is low? Are they gathering information about their partner's propensity to cooperate?

If such variation exists and animals can assess it, then cooperation in nature may have far more to do with partner choice (*9*) than with strategic reciprocity. So, in the theory of cooperation, has there been too much emphasis on reciprocity and too little on other factors? This is a question for future work to decide.

References

1. P. Hammerstein, in *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*, R. Noë, J. A. R. A. M. van Hooff, P. Hammerstein, Eds. (Cambridge Univ. Press, Cambridge, 2001), pp. 1–19.
2. D. W. Stephens *et al.*, *Science* **298**, 2216 (2002).
3. L. A. Dugatkin, *Cooperation Among Animals: An Evolutionary Perspective* (Oxford Univ. Press, New York, 1997).
4. R. Axelrod, W. D. Hamilton, *Science* **211**, 1390 (1981).
5. K. C. Clements, D. W. Stephens, *Anim. Behav.* **50**, 527 (1995).
6. G. Ainslie, *Picoeconomics: The Strategic Interaction of Successive Motivational States Within the Person* (Cambridge Univ. Press, Cambridge, 1992).
7. M. Mesterton-Gibbons, E. S. Adams, *Am. Sci.* **86**, 334 (1998).
8. R. H. Frank *et al.*, *J. Econ. Perspect.* **7**, 159 (1993).
9. R. Noë, in *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*, R. Noë, J. A. R. A. M. van Hooff, P. Hammerstein, Eds. (Cambridge Univ. Press, Cambridge, 2001), pp. 93–118.

PERSPECTIVES: GLACIOLOGY

Ice Sheets on the Move

Charles F. Raymond

As ice sheets retreated after the last glacial maximum, the ocean surface rose by more than 100 m, sometimes in pulses of more than a meter per century. Today, there are still large ice sheets in Greenland and Antarctica, and some of the remaining ice may be susceptible to release to the ocean.

The total mass of today's ice sheets is changing only slowly, and even with climate warming increases in snowfall should compensate for additional melting (*1*). Ice flow speeds can, however, change abruptly by orders of magnitude as a result of changes in lubrication at the ice base by pressurized water (*2*). Could ice be dumped directly into the ocean, possibly increasing the rate of sea level rise to much more than the present 0.2 m per century? Whether a threshold for such an event could be reached is a matter of ice dynamics.

The ice flowing out from ice sheets is focused into relatively narrow, faster moving paths deep in their interiors (*3*). These paths merge and accelerate toward the periphery, where they are called outlet glaciers (which follow deep valleys) or ice streams (which move on slippery beds between slow intervening areas). They typically reach the ocean by flowing into floating ice shelves. The grounded-floating transition is called the grounding line.

Increased melting is today resulting in ice shelf disintegration, thinning, and flow acceleration in some peripheral areas of Greenland and West Antarctica (*4*). Melting is likely to spread and intensify as the atmosphere and ocean warm. Could such boundary attack be propagated rapidly along fast-flow paths into the ice sheet interiors, "pulling" ice to the ocean (*5*)?

There is little evidence that the huge East Antarctic Ice Sheet is responding to recent climate warming. Certain marginal areas of the Greenland Ice Sheet subject to melting show large changes, but the interior remains in overall balance.

Although it is important not to lose sight of these major ice masses, the situation on the West Antarctic Ice Sheet (WAIS) is perceived as more serious (*6*). Its bed is well below sea level, and troughs guiding ice streams could provide corridors for grounding-line recession into the deep interior. Substantial melting on the upper surface of WAIS would occur only with considerable atmospheric warming, but increasing bottom melting of ice shelves could be important now.

The three major WAIS drainages show a mixed picture (*4*). The eastward drainage toward the Weddell Sea is close to mass balance now. The ice streams considered most threatening to WAIS stability drain northward to the Amundsen Sea (*7*). Over the last decade, this area has seen rapid recession of grounding lines, acceleration or widening of ice streams, and thinning over substantial distances back into the ice sheet (*8*). The causes are uncertain, but heat from the ocean may be the major factor.

There has been more extensive examination of both the history and dynamics of the westward drainage into the Ross Ice Shelf (see the figure). Over the last few centuries, margins of active ice streams migrated inward and outward, one ice stream (C) stagnated abruptly, and flow directions have shifted locally. Overall mass balance has changed from loss to gain (*9*). A currently active ice stream (Whillans)

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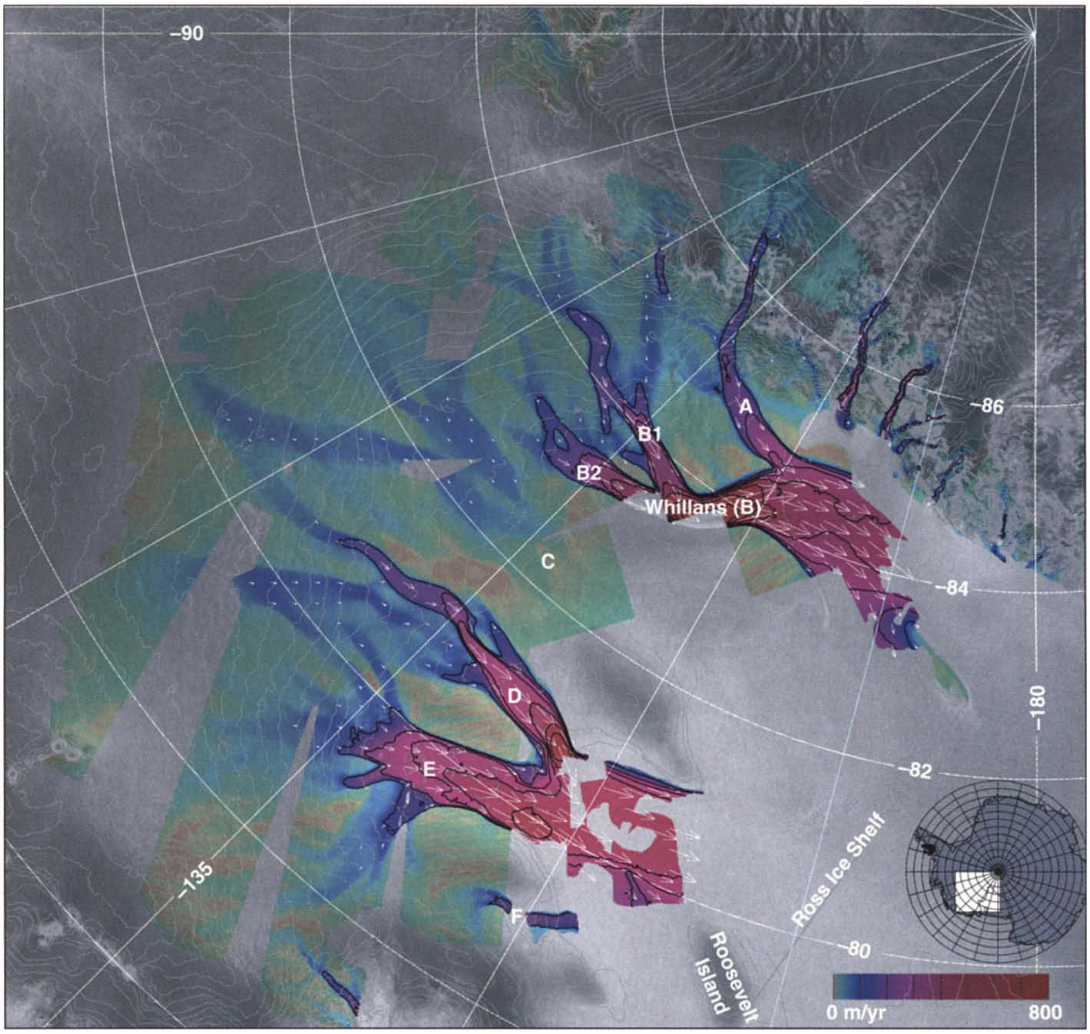

Tracking the flow of ice sheets. Synthetic aperture radar image, ice speed (color bar and black contours), and surface topography (gray contours) of the Ross Ice Shelf drainage of the West Antarctic Ice Sheet (index map) show a progressive concentration of westward flow from the deep interior toward the grounding zone with the Ross Ice Shelf (*17*). The ice streams in the outer parts of the grounded discharge paths have low slopes and associated gravitational driving force. They nonetheless move at high speeds over beds weakened by dilated till (*10*), with much of the gravitational force supported from the sides across marginal shear zones. The ice speed (*9*), surface topography (*3*), and image (*16*) derive from satellite data, which have revolutionized spatial coverage and resolution of remote ice sheets.

has slowed by about 20% over recent decades. This complex evolution may be associated with the late stages of Holocene retreat, with little influence from recent climate change.

The changes in Ross ice streams are providing new insights into regulation and thresholds for fast flow. The key element is extreme sensitivity of basal lubrication to water pressure through its effect on the strength of basal till (*10*). Because the ice streams are thin (~1 km) and their environment is cold, conduction of heat upward through the basal ice is expected to exceed the supply of geothermal heat in most cases. The streams would therefore freeze to their beds and stagnate if there were not compensating sources of heat or water.

Frictional heat is generated by the downslope ice flow and promotes positive feedback. As the ice speeds up, more heat and lubricating water are generated. However, this heat is not very effective in maintaining lubrication, because it appears only in limited quantities where the bed is already well lubricated (*11*). Rather, frictional heat is concentrated by stress transmission horizontally through the fast-moving ice toward the edges where the bed provides resistance. This effect tends to spread lubrication (*12*).

A water source is basal melt flowing from the deep interior, where ice is thick and basal melting is predicted (*13, 14*). The outward water flow can be redirected from beneath one ice stream to another as hydraulic potential responds to changes in the topography of the upper ice surface, thus switching fast flow on or off (*15*).

The spatial connections in basal lubrication provided by stress transmission in the ice and flow of basal water may explain how speed changes can spread over large areas from localized triggers. With regard to rapid sea level rise in a warming climate, the central and still unanswered question is how quickly flow acceleration can be initiated at low elevation and spread deep into the interiors of ice sheets. Understanding will be enriched by continued application of satellite, airborne, and ground techniques, especially to those areas in Antarctica and Greenland where flow speeds are now increasing. Practical methods to access and map subglacial conditions will be especially productive.

References and Notes

1. J. M. Gregory, J. Oerlemans, *Nature* **391**, 474 (1998).
2. Examples are glacier surges, Heinrich events, and changes in ice streams (described below).
3. J. L. Bamber, D. J. Vaughan, I. Joughin, *Science* **287**, 1248 (2000).
4. E. Rignot, R. H. Thomas, *Science* **297**, 1502 (2002).
5. T. Hughes, *J. Glaciol.* **38**, 125 (1992).
6. R. B. Alley, R. A. Bindschadler, in *The West Antarctic Ice Sheet: Behavior and Environment*, R. B. Alley, R. A. Bindschadler, Eds., vol. 77 of *Antarctic Research Series* (American Geophysical Union, Washington, DC, 2001), pp. 1–11.
7. T. J. Hughes, *J. Glaciol.* **27**, 518 (1981).
8. A. Shepherd, D. J. Wingham, J. A. D. Mansley, *Geophys. Res. Lett.* **29**, 1364, doi: 10.1029/2001GL014326 (2002).
9. I. Joughin, S. Tulaczyk, *Science* **295**, 476 (2002).
10. B. Kamb, in *The West Antarctic Ice Sheet: Behavior and Environment*, R. B. Alley, R. A. Bindschadler, Eds., vol. 77 of *Antarctic Research Series* (American Geophysical Union, Washington, DC, 2001), pp. 157–199.
11. S. Tulaczyk, W. B. Kamb, H. E. Engelhardt, *J. Geophys. Res.* **105**, 483 (2000).
12. H. P. Jacobson, C. F. Raymond, *J. Geophys. Res.* **103**, 12111 (1998).
13. B. R. Parizek *et al.*, *Geophys. Res. Lett.* **29**, 1214, doi: 10.1029/2001GL014326 (2002).
14. ——, *Geophys. Res. Lett.* **29**, 1682, doi: 10.1029/2002GL015704 (2002).
15. R. B. Alley *et al.*, *Ann. Glaciol.* **20**, 187 (1994).
16. K. C. Jezek, *Ann. Glaciol.* **29**, 286 (1999).

17. I thank I. Joughin for modifying the figure from (*9*).