id phase can emerge from the analysis of the expansion of the gas.

Is it possible to probe directly the emergence of superfluidity in these ultracold Fermi gases? Measuring the collective oscillations is not expected to be of great help in this respect. The frequencies of the collective oscillations can provide an accurate check of the consequences of unitarity, but cannot distinguish whether the hydrodynamic regime is due to superfluidity or to collisional effects.

To probe directly the occurrence of superfluidity, one should investigate other quantum effects. An important example is the study of rotational phenomena, in particular quantized vortices. In superfluid Fermi systems, vortices are characterized by quanta of circulation that are multiples of $\pi\hbar$, in contrast to bosons, where the quanta are multiples of $2\pi\hbar$. By generating a single vortex line, aligned along the symmetry axis of the trap, one should be able to generate a configuration with angular momentum per particle equal to $\hbar/2$. Configurations with single vortex lines have been realized with Bose-Einstein condensed gases, probing directly the quantization of circulation (*16*). Repeating such an experiment in a Fermi gas should provide a stringent test of superfluidity.

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PERSPECTIVES: BEHAVIORAL ECOLOGY

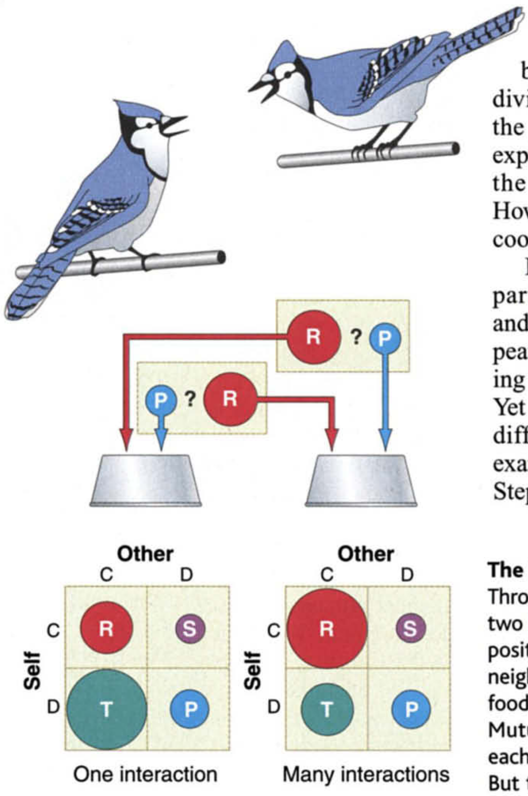
The Economics of Animal Cooperation

Michael Mesterton-Gibbons and Eldridge S. Adams

Human cooperation often depends on a delayed reciprocity in which each partner risks short-term costs to achieve a long-term mutual advantage. Are nonhuman animals capable of such cooperation? The evidence has been equivocal (*1*). However, in a set of clever experiments published on page 2216 of this issue, Stephens *et al.* (*2*) demonstrate that captive blue jays are indeed capable of sustained cooperation. Furthermore, the authors present evidence as to why it has been so difficult to observe sustained reciprocity in animal cooperation studies. In their experiment, a hungry bird can either cooperate or defect (that is, not cooperate) by selecting perches that control the allotment of seeds to itself and to a neighbor. Mutual cooperation allows both to obtain a large reward, whereas defection increases the immediate payoff to a selfish individual. By allowing food rewards to accumulate in clear trays before being released to the birds, the authors were able to control the degree to which their blue jay subjects preferred an immediate to a delayed reward (called discounting).

A large body of theory explores the potential for cooperation when there is a short-term temptation to cheat (*3*). Most of this theory builds on a thought experiment known as the Prisoner's Dilemma. In its simplest form, each of two individuals must "cooperate" (*C*) or "defect" (*D*)—that is, choose the option yielding the larger or the smaller payoff to the other. Mutual cooperation yields a higher reward (*R*) to each than does mutual defection (*P*) so that $R > P$ (see the figure). Yet each individual does better by defecting, regardless of the other individual's choice ($T > R$, $P > S$). So, in the absence of trust, each is tempted to exploit the other, and mutual defection is the only strategically stable outcome. How, then, can both enjoy the benefits of cooperation?

It has long been accepted that human partners can escape from this dilemma and sustain cooperation by interacting repeatedly and reciprocating (that is, matching the previous behavior of the other) (*4*). Yet such cooperation has been notoriously difficult to obtain in the laboratory. For example, in previous work, Clements and Stephens (*5*) exposed captive blue jays to



The Prisoner's Dilemma made simple. (Top) Through a system of levers and chutes, each of two hungry blue jays in adjoining cages can deposit either a large food item of value *R* in its neighbor's food tray (cooperation, *C*) or a small food item of value *P* in its own (defection, *D*). Mutual cooperation yields a higher reward to each than does mutual defection because $R > P$. But the temptation for each to exploit the other's cooperation by taking $R + P$ while the other gets nothing means that mutual defection is always strategically stable. **(Bottom left)** General reward matrix for a Prisoner's Dilemma: The rewards to one individual choosing *C* or *D* when the other chooses *C* or *D* satisfy $T > R > P > S$. The top part of the figure depicts the special case where $T = R + P$ and $S = 0$. **(Bottom right)** With a sufficient number of interactions, conditional cooperation increases the reward for mutual cooperation: Now $R > T$. But if the rewards reaped from cooperating are delayed, then the temptation to defect is eliminated only if $\alpha R > T$. Thus, as Stephens *et al.* (*2*) demonstrate, sustained cooperation may require both strategic reciprocity and sufficiently low discounting (sufficiently high α), that is, a sufficiently low preference for an immediate reward.

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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.

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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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