

value of -19.4 per mil (Fig. 2A). Both values indicate a diet predominantly composed of plankton; this is consistent with the site of collection, far from any significant area of marshes.

In summary, the stable isotopes of sulfur offer a valuable tool for tracing the flow of light sulfur produced during sulfate reduction in marine sediments. The sulfur in *Spartina* is isotopically light relative to the sulfur in plankton. The $\delta^{34}\text{S}$ values found in animals vary systematically in a manner that appears to reflect diet. The use of multiple isotopes, $\delta^{13}\text{C}$, $\delta^{34}\text{S}$, and $\delta^{15}\text{N}$, allows us to distinguish between three or more potential food resources.

The ribbed mussels in Great Sippewissett Marsh appear to obtain the bulk of their food from a source that is depleted in ^{34}S and enriched in ^{13}C . *Spartina* is the most likely source of this food, but it must be broken down to fine detrital particles before it is available to the mussels. Plankton appears to be the second major food resource, especially for the mussels near the main marsh channels connecting with Buzzards Bay. This finding supports the concept that marsh detritus is distributed along a gradient of maximum availability in the smallest marsh creeks to lower availability near the ocean (13), but there may be vertical gradients as well. As expected, there is no evidence for an important input of organic matter from the uplands, since Sippewissett is a pocket marsh with no major riverine input.

Where there is a major river input of organic matter, a combination of carbon, sulfur, and nitrogen isotopes can be used to discriminate between organic matter derived from the plankton, from salt-marsh plants, and from upland plants. The $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values of consumer organisms appear to reflect within about 1 or 2 per mil what they eat. This multiple isotope approach may help resolve long-standing questions about the role of salt marshes in the support of coastal fisheries and, in particular, the role of *Spartina* in providing detritus to marsh and estuarine consumers.

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2. The δ notation indicates the depletion (–) or enrichment (+) of the heavy isotope relative to the lighter isotope according to the formula $X = [(R_{\text{sample}}/R_{\text{standard}}) \times 10^3]$ where X is $\delta^{13}\text{C}$, $\delta^{34}\text{S}$, or $\delta^{15}\text{N}$ and R is $^{13}\text{C}/^{12}\text{C}$, $^{34}\text{S}/^{32}\text{S}$, or $^{15}\text{N}/^{14}\text{N}$. The standards are Pee Dee Belemnite for carbon, Canyon Diablo troilites for sulfur, and air for nitrogen.
3. Plant tissue samples for $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ were initially washed free of extraneous mud and debris. The tissues were dried at 70°C , then ground in a Wiley mill (1 mm mesh). Samples were washed in four 1-hour rinses of deionized water (4:1, water to sample). Samples were redried at 70°C . Plankton tow samples for $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ were collected in a 153- μm mesh nitex net. The sample was rinsed four times, first with tap water and then with deionized water in the 153- μm cod end of the plankton net. The sample was dried at 70°C . Animal tissue samples for $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ were prepared in a manner preventing gut and bone contamination. Animal tissue was dried at 70°C and then ground with mortar and pestle. Samples were washed in four 1-hour rinses of deionized water (4:1 water to sample). Samples were dried at 70°C . A subsample (>3 g, dry weight) was selected for $\delta^{34}\text{S}$ analysis. The remaining sample (>0.1 g for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) was washed in acid (10 percent HCl) for 1.5 hours to remove carbonate contaminants and again washed in deionized water. Samples of plant and animal tissues were examined for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ either at Geochron Labs, Boston, Mass., or at Global

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Mutual Restraint in Tree Swallows:

A Test of the TIT FOR TAT Model of Reciprocity

Abstract. *The TIT FOR TAT model of reciprocity, which is based on a successful program for the game known as the Prisoner's Dilemma, was experimentally tested on a population of tree swallows (Tachycineta bicolor). Parent and nonbreeding tree swallows have conflicts of interests that resemble those in the Prisoner's Dilemma. TIT FOR TAT predicts restraint of conflict before a competitor's act of defection, retaliation after defection, and a resumption of restraint following retaliation. After a simulated act of defection by nonbreeders, parents behaved as predicted by the model.*

Contemporary evolutionary biology has confronted the challenge of explaining the existence of cooperative behavior by invoking kinship (1) and reciprocity (2) theory. Empirical evidence, particularly from avian communal breeding systems, has generally supported kinship theory (3), although some studies (4) have revealed that the genetic relatedness of interactants is too low for kin selection to be the ultimate force maintaining cooperative behavior.

Until recently (4), reciprocity has received little attention in empirical studies of avian social systems because of the lack of a formal theory of reciprocity to adequately explain how it could first develop among unrelated individuals and then persist in competition with individuals that cheat in reciprocal arrangements (5). Axelrod and Hamilton (5) used game theory (6) and the concept of an evolutionarily stable strategy (ESS) (7) to develop a model of the evolution of

cooperation based on reciprocity. Their model is a solution to the familiar game Prisoner's Dilemma (8).

Prisoner's Dilemma is a symmetrical two-player nonzero sum game in which each player has the option to cooperate or defect during any interaction (9). Regardless of what a competitor does, a selfish act of defection receives a higher payoff than an act of cooperation. However, if both players defect, they do less well than if they both had cooperated (10).

When the game is played only once, the only ESS is to always defect, and cooperation is not favored (5, 11). During an iterated game the strategy called TIT FOR TAT becomes an ESS (5). To employ this strategy an individual initially cooperates and thereafter does whatever its competitor did on the previous move (12).

Because the TIT FOR TAT model can explain the evolution of cooperation

from an asocial state, it is especially appropriate to test the model on a social system in which cooperation is not fully developed but where antagonists frequently show restraint. I tested the model by examining the interactions between parent and nonbreeding tree swallows (*Tachycineta bicolor*) (13). Nonbreeding birds frequently visit the nests of breeders.

Tree swallows fulfill the three requirements necessary to play TIT FOR TAT (5); (i) they prefer to breed in aggregations, ensuring repeated interactions between the same individuals (14), (ii) they can recognize one another as individuals (15), and (iii) they display intraspecific aggression (13), including intraspecific killing (16).

Observations made from 1980 through 1983 revealed that nonbreeders were not cooperating with parents in the rearing of young (17). The banding of 519 birds showed that nonbreeders were never known close genetic relatives of breeders. It was hypothesized that nonbreeders were individuals in search of potential future nest sites (13). Thus, nonbreeders present several potential threats to parental reproductive success, including nest usurpation, disrupted feeding of young, stealing of food, and attraction of diurnal predators.

Given the conflict of interest between parents and nonbreeders, parents might be expected to display considerable hostility toward nonbreeders at their nests

(6). However, parental chase rates of nonbreeders were low (0.57 chase per hour) and 66.9 percent of 1175 parent-nonbreeder encounters were nonaggressive (17), suggesting that restraint is employed in this conflict of interests. A necessary precursor to the evolution of cooperation is restraint in conflict. TIT FOR TAT models restraint as well as fully developed cooperation (5).

An examination of the conflict between parent and nonbreeder genetic interests revealed a close resemblance to the Prisoner's Dilemma. Parents that increase their reproductive success by fledging as many young as possible and nonbreeders that learn the characteristics of suitable nest sites have a selective advantage over their competitors that do not. Parents showing restraint would allow nonbreeders to visit their nest boxes unhindered; an act of defection would prevent nonbreeders' visits by vigorous nest defense. For nonbreeders an act of restraint would be a benign visit or one in which they joined in the mobbing of a predator; an act of defection would be to behave in such a way as to lower parental reproductive success.

Parental defection (*T*) coupled with nonbreeder restraint (*S*) would reduce the probability of these nonbreeders being effective competitors with parents, or their offspring, for sites in the future by preventing nonbreeders from learning the characteristics of suitable nest sites (18). During mutual restraint (*R*), parents

gain potential nest site defenders and unthreatened reproductive effort; nonbreeders gain a knowledge of the location and characteristics of suitable nest sites, making them effective competitors for these sites in the future. Nonbreeder defection (*T*) coupled with parental restraint (*S*) results in the lowering of parental reproductive success and possible nest usurpation by nonbreeders (16). Thus, for both parents and nonbreeders $T > R$.

During mutual defection (*P*), nonbreeder actions lower parental reproductive success, and parents waste valuable time chasing nonbreeders. Nonbreeders can gain by reducing the number of potential competitors. For both parents and nonbreeders the payoff for this is greater than showing restraint when the other defects ($P > S$). But, with the assumption that decisions are generally based on the average of past outcomes (19), if nonbreeders commonly defected, parents would be more apt to be aggressive toward them (20). This would reduce the probability of nonbreeders being able to familiarize themselves with nest sites. Consequently, parents and nonbreeders can do less well when they both defect than when there is mutual restraint ($R > P$), thus satisfying the inequalities that define the Prisoner's Dilemma matrix (6, 10).

To test the TIT FOR TAT model, I cast parents and nonbreeders in the parts of players and simulated an act of defection by nonbreeders by making it appear as though nonbreeders had killed nestlings (16). On nestling day 16 (21), I presented breeding pairs with two stuffed model nonbreeders simultaneously (22). When the parents returned to their nest box, I recorded their responses (23) to the models for 5 minutes. I then replaced two live nestlings with two dead 16-day-old nestlings. The dead nestlings were placed on their backs on the nest cup rim. After parents returned, and entered and exited their boxes, I recorded their responses to the models for another 5 minutes. As a control, I repeated the same procedure on nestling day 12, but instead of replacing live nestlings with dead ones, I merely banded the young present (24).

A sign test (Table 1) showed that during the control portion there was no statistically significant difference in parental responses to the models before and after the banding of nestlings. These results indicate that I, as the nestling manipulator, did not elicit responses from the parents that were redirected at the models.

After the placement of dead nestlings,

Table 1. Sum of hover, dive, and contact responses by both tree swallow parents in the TIT FOR TAT experiment. In the control sequence, the young were banded between the two series of observations, and in the experimental sequence, two live nestlings were replaced by two dead ones. The sign test indicates that parental responses to nonbreeding birds before and after manipulation of young in the control sequence do not show statistically significant differences ($n = 8$, $x = 1$, $P = 0.0703$), whereas those before and after replacement of the nestlings do ($n = 13$, $x = 12$, $P = 0.0034$).

Nest box	Control			Experiment		
	Number of responses		Sign of difference	Number of responses		Sign of difference
	Before	After		Before	After	
242	*	*	*	3	7	—
126	*	*	*	4	6	—
129	0	0	0	2	6	—
127	4	0	+	0	1	—
30	0	0	0	*	*	*
133	5	0	+	1	0	+
23	0	0	0	0	5	—
257	1	0	+	0	0	0
34	1	0	+	0	0	0
26	0	0	0	0	0	0
117	0	0	0	0	1	—
245	1	0	+	0	3	—
243	6	1	+	0	5	—
265	0	1	—	0	2	—
31	0	0	0	0	6	—
14	0	0	0	0	1	—
29	1	0	+	0	0	0
122	0	0	0	0	5	—

*Trials in which parents did not return to the boxes and enter within 60 minutes after manipulation.

12 of 17 pairs gave results consistent with the prediction of retaliation following defection (5). One pair gave results in contradiction to this prediction, but their response was a brief nonaggressive hover above a model. A sign test showed statistically significant differences in responses before and after replacement of the nestlings (Table 1). Parents that responded to the models after the placement of dead nestlings did not redirect their aggression at their mates or at neighboring breeding pairs. Parents also chased live nonbreeders during the experiment. But, live nonbreeders were ignored if their time of appearance at the nest box precluded the possibility of their committing the defection.

Parent tree swallows displayed the characteristics of the TIT FOR TAT strategy by (i) acting "nice" to the model nonbreeders until after the simulated defection, (ii) being provoked into defecting, and (iii) appearing "forgiving": a significantly larger proportion of encounters (27 of 82) ended in parental chases of nonbreeders before the simulated defection ($z = 2.58$, $P < 0.01$) than did encounters after the simulated defection (18 of 110) at those boxes where parents responded to the models after the simulated defection (25). This result indicates a return to normal behavior by the birds in the experiment because parental aggression toward both model and live nonbreeders decreased as the breeding season progressed at boxes outside the experiment (13).

These results suggest that the TIT FOR TAT strategy adequately models the restraint shown in the conflict of interest between parent and nonbreeder tree swallows, and that TIT FOR TAT may be fruitfully applied in the analysis of other phenomena in which the genetic relatedness of interactants is inadequate to explain the restraint of conflict demonstrated by the interactants.

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7. An ESS is a strategy such that if all of the members of a population adopt it no mutant strategy can invade (6).
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9. A nonzero sum game is one in which the interests of the players are not in direct conflict, making it possible for both players to gain or lose during an interaction. After each interaction, each player receives a payoff that is not only dependent on its own actions but also on those of its competitor. In a biological context, payoffs are in terms of the effects a player's actions have on its fitness [(5); S. Riechert and P. Hammerstein, *Annu. Rev. Ecol. Syst.* 14, 377 (1983)]. Gains or losses are in terms of the payoffs assigned to the outcome of an interaction (6). In a symmetrical game the payoffs to each player are equal (6). The requirement of symmetrical payoffs can be relaxed as long as the inequalities that define the payoff matrix describing Prisoner's Dilemma are met. Payoffs need only be measured in terms relative to one another [R. Axelrod, *The Evolution of Cooperation* (Basic Books, New York, 1984)].
10. Each player receives a payoff R (reward) for mutual cooperation. But each player is "tempted" to defect because doing so against a cooperative competitor results in the highest payoff T (temptation to defect). In this case, the cooperator receives the lowest payoff S (sucker's payoff). However, if both defect each gets the payoff P (punishment for mutual defection) that is less than R . The payoff matrix is defined by $T > R > P > S$ and $R > (T + S)/2$ (5, 8).
11. This is also the solution in biological evolution (5). In effect, cooperators quickly go extinct in competition with defectors.
12. A player using TIT FOR TAT is (i) "nice" in that it is never the first to defect, (ii) provokable into a defection by a defection by its competitor, and (iii) "forgiving" in that it only punishes its competitor once for a defection and is willing to play again without an act of restitution (5).
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21. On average, fledging = nestling day 20 (13).
22. One model was of adult, iridescent blue-green, breeding plumage representing all after-hatching year (AHY) and male nonbreeders and some second year (SY) and all third year (TY) and older female nonbreeders. The second model was of immature, brown plumage meant to represent all AHY and some SY female nonbreeders and all hatching year nonbreeders. Models were presented together so that parental responses were not biased by model-nonbreeder sex, or age, or both. The models were attached to sticks positioned 2 m apart and 1 m from the front of the nest box. Each model was an equal distance from front of the nest box. Each model was an equal distance from the nest box hole. Sticks were 1 m high. Model position, to the right or left of the hole, was determined by a coin flip before each trial.
23. Responses measured were hovers, dives, and contacts (for example, pecks at the model or pulling of feathers from the model).
24. There was no statistically significant change in parental aggression toward live nonbreeders between nestling days 12 and 16 at boxes outside of the experiment (13).
25. Difference between proportions test [J. H. Zar, *Biostatistical Analysis* (Prentice-Hall, Englewood Cliffs, N. J., 1974)].
26. I thank H. W. Power, R. Axelrod, W. D. Hamilton, J. D. Ligon, and the reviewers for their criticisms on various versions of the manuscript. The Town of Oyster Bay, N.Y., allowed me to use the J. F. Kennedy Memorial Wildlife Refuge at Tobay Beach as a study site. Supported by the F. M. Chapman Fund of the American Museum of Natural History, Sigma Xi, the Northeastern Bird Banding Association, the Ecology Graduate Program, and a J. Leatham grant from the Zoology Program at Rutgers University.

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Response to Ethanol Reduced by Past Thiamine Deficiency

Abstract. *Ethanol-induced intoxication and hypothermia were studied in rats approximately 7 months after severe thiamine deficiency, when treated rats appeared to have recovered their physical health. Previously induced thiamine deficiency without prior ethanol exposure significantly decreased the area under the curve plotted for the concentration of ethanol in blood and also decreased behavioral impairment and hypothermia due to ethanol exposure. Pathophysiologic changes resulting from thiamine deficiency may contribute to both the pharmacodynamic and pharmacokinetic tolerance to ethanol in chronic alcoholics.*

Alcoholism is characterized by progressive increases in consumption of alcoholic beverages with concomitant alterations in the metabolism of ethanol and its effects on the central nervous system (tolerance) (1). Long-term exposure to ethanol can also result in physical dependence (1) and chronic pathologic changes in many organ systems (2). Alcoholism is frequently associated with thiamine (vitamin B₁) deficiency resulting from inadequate nutritional intake, decreased absorption, or impaired utilization (3). The contribution of thiamine deficiency to ethanol toxicity and the resultant dysfunction in organ systems remains controversial (4).

Wernicke's encephalopathy is an acute neuropsychiatric syndrome caused by thiamine deficiency most often found in the nutritionally compromised chronic alcoholic (5). Treatment with thiamine reverses most of the acute manifestations (5), but clinical abnormalities such as memory loss, apathy and social indifference, superficial and labile emotions, and lack of goal-oriented spontaneous activity (Korsakoff's psychosis) may persist together with neurochemical disturbances (5, 6). Characteristic neuropathologic findings at autopsy include bilaterally symmetrical periventricular lesions of the brainstem and diencephalon (5, 6).