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symbiont assemblage to more thermally tolerant zooxanthellae genotypes (26–28), could increase the tolerance of reef-building corals to future ocean warming. However, existing data suggest that symbiont shuffling to thermally tolerant genotypes would increase thermal tolerance by 1° to 1.5°C, which is insufficient to cope with the magnitude of SST change predicted for the Red Sea and much of the tropical oceans over this century (29). Indeed, our data do not suggest that *D. heliopora* has acquired enhanced resistance, despite a decade of exposure to persistent thermal stress. Continued efforts to quantify the thermal tolerances of other coral species and important reef calcifiers will improve our predictions of how climate change will affect coral reefs of the central Red Sea. However, the data in hand suggest that without immediate, aggressive global intervention to reduce carbon emissions below IPCC A1B and A2 scenarios, the pressures of predicted annual heat stress will most certainly result in further deterioration of coral health in the central Red Sea over this century.

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Shared Social Responsibility: A Field Experiment in Pay-What-You-Want Pricing and Charitable Giving

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A field experiment ($N = 113,047$ participants) manipulated two factors in the sale of souvenir photos. First, some customers saw a traditional fixed price, whereas others could pay what they wanted (including \$0). Second, approximately half of the customers saw a variation in which half of the revenue went to charity. At a standard fixed price, the charitable component only slightly increased demand, as similar studies have also found. However, when participants could pay what they wanted, the same charitable component created a treatment that was substantially more profitable. Switching from corporate social responsibility to what we term shared social responsibility works in part because customized contributions allow customers to directly express social welfare concerns through the purchasing of material goods.

In a provocative article some 40 years ago, Milton Friedman stated that “the social responsibility of business is to increase its profits” (1). According to this view, private companies should focus on the provision of profits for shareholders, leaving the provision of public goods to

others. The boldness of the prescription provoked a countermovement in favor of broad social consciousness from private companies to prioritize corporate social responsibility (CSR).

Today CSR is practiced by many firms worldwide, yet often CSR-related costs are higher than their commercial benefits (2). Two major factors may contribute to this limited success. First, customers might assume that CSR practitioners have ulterior motives (3). Consider a company choosing between high- and low-cost manufacturing options (e.g., using recycled or natural resource-intensive materials). The “good,” CSR-

consistent, option is profitable only if it generates enough customer interest to offset increased costs. However, if consumers are suspicious of the firm’s intentions, the goodwill behind CSR may appear to be just another consumer manipulation (4).

Second, CSR purchases send a weak signal to oneself and to others regarding the buyer’s “social intentions.” People identify with the social causes they support, but purchasing from a CSR-oriented company leaves that cause too remote from their core identity. Buying a pair of shoes from an ecologically friendly company sends a signal (to self and to others) that the customer cares about the environment, but it also sends a signal that the customer simply likes the shoes. What part of the purchase reflects style consciousness, and what part reflects social consciousness?

We propose a new CSR strategy, which we term shared social responsibility (SSR). To improve programs based on social preferences, companies need to specifically engage the social preferences of their consumers. If social responsibility is to provide any benefit to a company, its customers, and the community, it should go beyond the priorities of the firm and instead express the priorities that the firm shares with its customers.

For our investigation we used a recently emerged pricing strategy hinging on the social preferences of customers, referred to as “pay what you want” (PWYW). In this strategy, in

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lieu of a fixed price, a firm offers a good or service for whatever price customers want to pay (typically including \$0). If people only cared about money, they would pay the lowest price possible, yet in practice people frequently pay more (5–7).

We created a SSR situation through the combination of PWYW pricing and CSR. When paired with corporate giving, PWYW may help the firm mitigate the aforementioned problems; because the firm explicitly exposes itself to financial risk, a customer is unlikely to infer sinister ulterior motives. Thus, we used a pricing strategy that reduces customers' concerns about ulterior motives while also enhancing their identification with the cause, as every dollar spent directly reflects this self-identification. The design does not test the individual contributions of these two possible shortcomings of CSR, but by reducing both, SSR offers a plausible alternative to traditional CSR efforts.

Taken from a different perspective, SSR should also benefit the effectiveness of PWYW. It is theorized that the effectiveness of PWYW hinges on how much a consumer wants the good or service, as well as on how much he or she

wants to help the company. Under the proposed SSR method, each purchase directly represents the customer's desire to support both the company and the charitable partner.

We conducted a field study at a large amusement park (8). Participants ($N = 113,047$) rode a roller coaster–like attraction, were photographed during the ride, and later chose whether to purchase a print of the photo.

We used a 2×2 between-participants design. The first dimension was the price of the picture (either a regular \$12.95 price or PWYW). The second dimension was Charity (either no charitable contribution or half of the revenue going to charity). The charitable partner was a nationally recognized patient-support foundation. Each of the four treatments was conducted over two full days.

The results of the two fixed \$12.95 price conditions reveal low and similar purchase rates (0.50% without charity, 0.59% with). PWYW substantially increased purchase rates to 4.49% in the PWYW + Charity treatment and to 8.39% in the simple PWYW treatment. In the PWYW treatments, buyers paid significantly more per photo when half of the revenues went to charity

($M = \$5.33$ per photo) than with no charity [$M = \$0.92$; $t(3535) = 43.24$, $P < 0.001$ (9)]. Figure 1 presents the resulting profits.

Despite the observation in the literature that CSR is not profitable, many companies (including the one in question) contribute substantially to charity independent of specific product promotions. Accordingly, we identify all post-cost revenue as profit. By this account, both Charity treatments are the most profitable, and a t test confirms that SSR is substantially more profitable than traditional CSR ($M_{\$12.95+Charity} = \0.071 per rider versus $M_{PWYW+Charity} = \$0.198$ per rider; $P < 0.001$) (9).

With more than 5 million riders per year, there is a potential annual increase of more than \$600,000 in profits. Does increased photo purchasing crowd out spending elsewhere in the amusement park (e.g., for popcorn or gifts)? Clearly, if SSR merely cannibalizes another element of the business, we should be more circumspect in our inferences. Although we cannot speak to every possible case of crowding out, our data suggest that this is not the case. Immediately after leaving the photo area, customers passed through a merchandise area (containing T-shirts, keychains, etc.). Total sales data from those days (Table 1) suggest that increased photo revenue does not lead to decreased merchandise revenue in the immediate store, but future research is needed to thoroughly investigate the incidence of product cannibalization.

SSR increased profit, perhaps because it minimized suspicion of the firm's intentions and maximized the identity expressiveness in the purchase. This contention is further supported by an intriguing piece of evidence in the purchase rates of PWYW and PWYW + Charity customers: The addition of the charitable promotion actually suppressed purchasing [$\chi^2 = 336.17$, $P = 0.001$ (9)]. This is consistent with our explanation that with fixed prices, customers buy only when the benefits outweigh the costs. In the PWYW + Charity condition, the cost of sending a bad signal looms large, so customers with a low value for the picture will prefer not to buy it over buying it either for a low price (bad signal) or for a high price (not worth it).

Historically, company ethics are seen as competing with company economics (10–14), but our study suggests a method in which the pursuit of social good does not undermine the pursuit of profit. Under SSR, the consumer chooses a price, thereby actively determining his or her contribution to the cause. Apparently, a company can best serve its community and its shareholders by sharing its social responsibility with its customers.

Fig. 1. Profit per rider (amount paid minus production costs). Photo sales were most profitable for the firm and made the largest contribution to charity when participants could pay what they wanted and half of their payment went to charity—the shared social responsibility treatment.

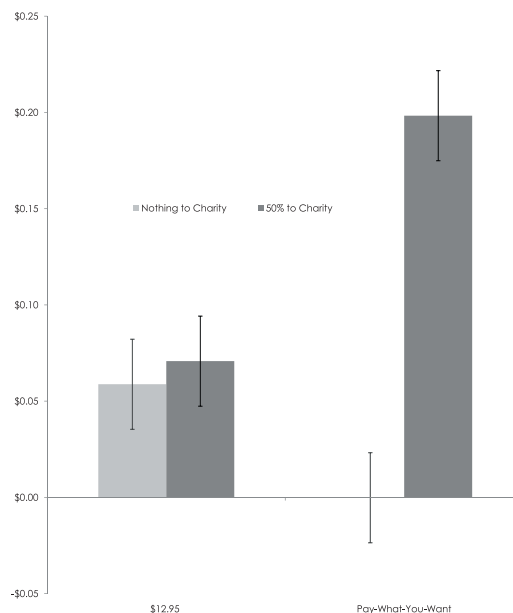


Table 1. Treatment effects on photo revenue and merchandise revenue. Merchandise refers to items such as souvenir keychains whose prices were not directly manipulated in the experiment. There were essentially no differences in merchandise sales over the same days. If anything, people spent slightly more on merchandise in the PWYW + Charity condition. We can likely rule out concerns that increased photo revenue was cannibalizing from other sources.

Treatment	Photo revenue	Merchandise revenue	Riders	Merchandise revenue per rider
\$12.95	\$1823	\$11,280.98	28,224	\$0.40
\$12.95 + Charity	\$2331	\$12,322.72	30,592	\$0.40
PWYW	\$2175.80	\$11,833.90	28,263	\$0.42
PWYW + Charity	\$6224.22	\$11,694.03	25,968	\$0.45

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The Structure of *cbb₃* Cytochrome Oxidase Provides Insights into Proton Pumping

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The heme-copper oxidases (HCOs) accomplish the key event of aerobic respiration; they couple O₂ reduction and transmembrane proton pumping. To gain new insights into the still enigmatic process, we structurally characterized a C-family HCO—essential for the pathogenicity of many bacteria—that differs from the two other HCO families, A and B, that have been structurally analyzed. The x-ray structure of the C-family *cbb₃* oxidase from *Pseudomonas stutzeri* at 3.2 angstrom resolution shows an electron supply system different from families A and B. Like family-B HCOs, C HCOs have only one pathway, which conducts protons via an alternative tyrosine-histidine cross-link. Structural differences around hemes *b* and *b₃* suggest a different redox-driven proton-pumping mechanism and provide clues to explain the higher activity of family-C HCOs at low oxygen concentrations.

In all organisms, energy is stored in electrochemical ion gradients across biological membranes and used for solute transport and for synthetic processes like adenosine triphosphate (ATP) synthesis. Electrochemical gradients are mainly generated by vectorial membrane reactions—for example, electron transfer from one side of the membrane and proton uptake from the opposite side—and/or by pumping ions, normally protons, across the membrane using the energy of light or of chemical processes such as ATP hydrolysis or redox reactions. How proton pumps function on an atomic scale has been a central theme of bioenergetics for three decades.

Heme- and copper-containing terminal oxidases (HCOs) function as cytochrome *c* oxidases or as quinol oxidases in aerobic respiration but also play a role in oxygen scavenging and in maintaining redox homeostasis by coupling the exothermic four-electron reduction of O₂ to H₂O with proton pumping (1, 2). Experiments on these integral membrane protein complexes are, however, severely hampered by a complex reaction cycle involving eight protons (four pumped plus four consumed), four electrons, and O₂, and the fact that both pumped and consumed protons contribute to the formation of the electrochemical

gradient. Therefore, processes such as the coordination of electron transfer and proton pumping without wasting energy, the kinetic barriers that ensure unidirectional productive proton transfer, and the nature of the gates that separate protons that are consumed in water formation from those that are pumped are far from understood (1, 3).

HCOs are diverse in terms of subunit composition, electron donor, and heme type, resulting in different electron and proton transfer characteristics. However, they share a central subunit built up of 12 membrane-spanning helices ($\alpha 1$ to $\alpha 12$) that contains a low-spin heme (*a* or *b*) and a high-spin heme (*a₃*, *o₃*, or *b₃*)–copper (Cu_B) binuclear center to which O₂ is bound and reduced during the catalytic cycle. Based on overall amino acid similarities of the central subunit and specific differences of the proton channels, the HCO superfamily is subdivided into three major families: A, B, and C (4). The A HCOs, which comprise the mitochondrial and many bacterial cytochrome *c* oxidases, and the B HCOs require, in addition to the central subunit, at least one other subunit (II), which usually contains a binuclear Cu_A center to channel electrons toward the buried O₂ binding site. Whereas family-A HCOs use at least two proton pathways (5), B HCOs appear to use only one (6). The prototypes of family C, comprising ~20% of HCOs (7), are the *cbb₃* oxidases. These are characterized by reduced proton pumping (8) and by a higher catalytic activity at low oxygen concentrations [the Michaelis constant (*K_M*)

for O₂ of ~7 nM is lower by a factor of 6 to 8 than that determined for family-A HCOs (9)]. This property is exploited in nature (10) by many pathogenic proteobacteria that colonize microaerobic host tissues and by agronomically important symbiotic diazotrophs that can simultaneously perform aerobic respiration and nitrogen fixation, which involves an oxygen-sensitive nitroreductase. Interestingly, *cbb₃* oxidases also reduce NO to N₂O (11). Family-C HCOs contain the central subunit (N) and either one (O) or two (O + P) additional subunits that are completely different from family A and B subunits. Subunits O and P contain one- and two-heme C molecules, respectively, and are predicted to possess cytochrome *c* folds (7, 12, 13). Because some family-C HCOs, similar to the evolutionary closely related NO reductases, are composed of only subunits N and O, these are defined as the core complex (14). Family-C HCOs optionally associate a fourth subunit (Q) that is involved in stabilizing the interactions of subunit P with the core complex at least in *Rhodobacter capsulatus* (15).

We crystallized the *cbb₃* oxidase from the bacterium *Pseudomonas stutzeri* strain ZoBell using pentaerythritol ethoxylate as precipitant and a dodecyl- α -D-maltoside/decanoilysucrose/undecyl- α -D-maltoside detergent mixture. Its structure was determined by applying the favorable anomalous properties of iron for phase determination [see supporting online material (SOM)]. We independently determined the sequences used for model building because published sequences (12) were not compatible with the results of our mass spectrometric analysis (see SOM and fig. S1). The reliability factors *R* and *R_{free}* of the refined structure were 18.3% and 22.4% in the resolution range 10 to 3.2 Å. *Cbb₃* oxidase has a size of about 45 by 65 by 100 Å, with subunit N localized in the membrane and subunits O and P predominantly in the periplasm (Fig. 1). Despite the low sequence identity [pairwise below 20%, overall 4% (fig. S1)], subunit N has the expected architecture of the central subunit (16, 17) indicated by low root mean square deviations [2.5 to 3.0 Å (fig. S1)] between subunit N and the other structurally known HCOs [A-family *Paracoccus denitrificans* (5, 18, 19), *Rhodobacter sphaeroides* (20, 21), bovine heart (22) cytochrome oxidases, and *Escherichia coli* quinol oxidase (23), as well as the B-family *Thermophilus thermophilus* cytochrome oxidase (24)]. The analysis of the interactions between the protein and the high-spin heme *b₃*, and low-spin heme *b* in

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