(as Owen and Wiegert would predict), the survivorship of others *in the same sward* is decreased. There are too many complex situations in which grazing alters the *relative* abundance of *different* grass species for it to be likely that any general hypothesis which states that all grasses have evolved a dependence upon grazers for survival is correct. Intermittent grazing may be as necessary to allow a diversity of grasses to coexist at a site as it is to prevent the invasion of grassland by trees, but there is nothing about these observations which necessitates an evolutionary explanation involving mutualism with grazers.

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Grasses, grazers, mutualism, and coevolution: a comment

Carlos M. Herrera, Estación Biológica de Doñana, Sevilla-12, Spain

Owen and Wiegert (1981) have recently suggested the hypothesis that grasses and grazers represent a highly coevolved system which has developed on the basis of a mutualistic relationship. They interpreted the findings by Dyer and Bokhari (1976) and Dyer (1980) that saliva produced by grazers stimulates grass growth as a mutualistic adaptation by which both grass and grazers benefit, and later put this into the context of the more general hypothesis that plant feeders can in a variety of ways maximize the fitness of the plants they eat (Owen and Wiegert 1976, Owen 1980). Their interpretation of growth enhancement by saliva as a mutualistic process leading to coevolution is however questionable and I wish to point out here that their arguments do not support convincingly the proposed hypothesis.

Individuals of the two kinds participating in a mutualistic relationship must have greater fitness than those of its own kind which do not, all else being equal. In other words, some evolutionary advantage in terms of differential reproduction must be derived to genotypes by the very act of interacting with individuals of the mutualistic counterpart. If grasses and grazers exemplify a true mutualistic system it is indispensable to demonstrate that grazed grasses and stimulatory saliva-producing herbivores have higher fitness than ungrazed grasses and stimulatory saliva nonproducers, all else being equal. I feel that Owen and Wiegert have failed to prove this.

Advantages to the plants

Owen and Wiegert's arguments in support of the greater fitness of grazed plants are, at best, extremely loose. They write "... what is the advantage to the individual plant? The answer seems obvious: the grass plant increases its productivity. But grazing, although promoting grass growth, tends to reduce seed production. This

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difficulty can be resolved if, as we believe, grazing prolongs the life of the individual genotype and the absence of grazing, although allowing a short-term increase in seed production, results in the early death of the individual plant, thus in the long-term decreasing fitness". They latter added that "grazing, of course, tends to inhibit flowering and seed formation. Short-term fitness is reduced but the genotype becomes very large and very old, and in the long-term its fitness is enhanced". To my opinion, Owen and Wiegert have relied on some intuitive assessment of differential long- and short-term fitness without ever providing a precise definition of what they meant by short- and long-term fitness, and on which time scale are they measuring it. Although they explicitly use fitness as "the contribution to the next generation of one genotype in a population relative to the contribution of others", they actually place more emphasis on differential mortality rates than on differential reproductive success, and they underscore the significance of substantially different generation times in their comparisons of reproductive value.

Let us consider a mixed grass population made up of genets differing in their response to grazers' saliva. "Saliva-responsive" genets will increase their productivity, while "nonresponsive" ones will not, following damage by herbivores. In terms of offspring produced it is far from clear that saliva-responsive genets will always contribute more genes to the "next" generation than nonresponsive ones. In fact, it is necessary to know how long this generation is in absolute time units for the two types of genets and, in the most extreme cases, if that "next" generation will really ever come to responsive gents (see McNaughton 1979, Cook 1979). Nonresponsive genets will grow less and have shorter generation time but will probably produce more seeds *per any arbitrary time unit.* Summed over any given time period, short-generation nonresponsive genotypes, their offspring, and their offspring's offspring will have produced altogether far more seeds than long-generation responsive ones. If all seeds produced by both genotypes successfully germinate and reach the reproductive stage, long-lived responsive genotypes would be at a disadvantage. This is not the case in nature because on the long run grazers probably would eliminate differentially the two types of genets from the population, thus decreasing the fitness of short-lived ones. The final result would be a mixed population with relative frequencies of the two responsiveness types (and, hence, generation length) depending on grazing frequency and intensity. In this polymorphism it is far more complicated than presented by Owen and Wiegert to predict a consistently superior fitness among saliva-responsive genotypes.

Grazing pressure may be very high, and in this case saliva-responsive genotypes would eventually become dominant and the nonresponsive one completely eliminated from the scene or reduced to extremely low frequencies. This situation is the one Owen and Wiegert are apparently referring to throughout their paper. In this extreme situation, the few surviving saliva-responsive genets become larger and larger, and are virtually immortal (generation time tending to infinite, mortality rates tending to zero, and reproductive output near to zero in equilibrium populations). What would happen if a mutant strain arise in this "fossilized" population of growth-responsive individuals which, according to Owen and Wiegert, have maximized their fitness by virtue of being heavily grazed? Assume that the mutant strain is similar in all other respects to the remainder of the population (including the saliva-responsiveness trait), but that is able to deter herbivores as a consequence of possessing some heritable character (e.g. powerful chemical defences). The new, short-lived genotype could devote a greater proportion of energy and nutrients to reproduction, and would therefore be able to produce many more offspring per genet and time unit than the palatable dominant genotype. The fitness of the new genotype would thus be higher and almost certainly it would eliminate the old strain even under heavy grazing pressure, provided herbivores do not overcome its defences. There is no room to argue that the unpalatable genotype is increasing its "short-term" fitness while the palatable, grazed genotype is maximizing its "long-term" fitness. What in fact occurs is that recurrent grazing had favoured very long generation times among grasses susceptible to grazers as a way of increasing the chances of reproduction (e.g. by "waiting" for temporary opportunities provided by grazers' predators and parasites), but that as soon as a grazer-resistant genotype arose having a shorter generation time and greater reproductive potential per time unit, the latter had the evolutionary advantage. Is there actually any mutualism if, all else being equal, one may easily envisage mutualistic (grazed) genotypes being led to extinction by nonmutualistic (ungrazed) ones?

Advantages to grazers

Owen and Wiegert suggest that "the special properties of the saliva have been evolved by selection by grasses on grazers". They suggest that the offspring and relatives of stimulating-saliva-producing (SSP) grazers will take advantage of the greater productivity created by earlier grazing, provided that parents and offspring inhabit the same general feeding grounds.

In a population of grazers consisting of individuals differing genetically with respect to the SSP habit, increased productivity will normally also benefit the offspring and relatives of non-SSP genotypes, or even to different species. In other words, a mutation affecting an entirely non-SSP population and leading to the appearance of one or a few SSP genotypes will favour not only the bearers of the SSP trait and their relatives, but also will benefit unrelated, non-SSP individuals by roughly the same amount, unless families and individuals of grazers strictly partition grazing grounds intra- and interspecifically from generation to generation in a constant fashion and/or maintain the same exclusive feeding territories for most of their lives. Patterns of resource use bearing some resemblance to this have been demonstrated for very few vertebrate herbivores (Wilson 1975) and among invertebrate herbivores territoriality seems to be extremely rare (Otte and Joern 1975). As no relative advantage to SSP individuals will derive from the possession of the SSP trait, it is highly unlikely that the SSP habit will spread in the population and become dominant by "selection on grazers by grasses" only, as suggested by Owen and Wiegert. This gene could, of course, spread for reasons unrelated to selection by grasses as, for example, that promoting grass growth is an incidental consequence of the saliva having improved digestive efficiency.

Consider also the time scale on which the feedback grazer-saliva-grass-grazer occurs. By the action of grazing, a SSP grazer will promote the growth of a given patch of grass, which will take place within a few days or weeks after feeding (McNaughton 1976). For this same individual grazer or its relatives to receive the benefits of its salivary induction, it is necessary that the saliva-induced grass patch remains unvisited by other herbivores over that period. In the case of African large migratory herbivores mentioned by Owen and Wiegert, the delay between the initial feeding and the return to saliva-stimulated grass patches will be too long to expect that no other grazers have touched upon stimulated grass. In a paper overlooked by Owen and Wiegert, McNaughton (1976) nicely showed that increased grass production originated by wildebeest grazing do not benefit to these ungulates, but to Thomson's gazelles arriving at the area after the departure of wildebeest herds. Without invoking some sort of interspecific altruism, how could grasses have selected for the SSP habit among wildebeest if the derived benefits go to gazelles?

I have been assuming so far that the SSP habit does not have any especial energetic or nutritional costs to the grazer. If the growth-stimulating substance is an ad hoc production to estimulate grass growth, with no further digestive significance to the herbivore (which is essential to admit that the SSP habit has been selected by plants by virtue of its mutualistic function only), then the SSP habit has a definite and measurable cost to the herbivore. In this case, and provided that the benefits are not restricted to the individual which supports the costs of production or its relatives, the spread of the SSP habit in the population by selection of grasses on grazers becomes still more unlikely (see Tullock 1979 for a discussion of "public goods" in nature). Drawing a rough analogy with human economy, what advantages could derive to a farmer who spends money and efforts in fertilizing a pasture, and later has it open to grazing cattle owned by non-reciprocating neighbouring farmers?

Predator-prey-like coevolution

Arguments above do not go against the notion of grasses and grazers representing a coevolved system, but rather against the suggestion that the coevolutionary process relies on mutualistic, saliva-mediated relations. Some grass traits quoted by Owen and Wiegert as indicative of mutualism had been previously interpreted in the light of a predator-prey-like coevolved system (e.g. McNaughton 1976, 1978, 1979, Caughley and Lawlor 1981). Nevertheless, Owen and Wiegert plainly considered that grasses do not defend themselves from grazers. In their opinion, "there is no question of grasses defending themselves grom grazers", and they "do not envisage grasses as chemically defending themselves against grazers". As they put it, it is more of a matter of opinion than of a belief based on evidence. Owen and Wiegert's opinions notwithstanding, grasses do have traits unequivocally suggesting defensive functions and, as suggested by Caughley and Lawlor (1981), "plant defences attest the obvious: being eaten is usually a bad thing".

The presence of silica particles (phytoliths) in grass blades and stems, apparently lacking any supporting function, must represent a serious defensive weapon aimed at abrading the teeth of grazers. Scanning electron photomicrographs of these phytoliths reveal a variety of sizes and shapes but they invariably have edges conspicuously resembling files or saws (see e.g. Gueguen et al. 1975, Cherouyrier et al. 1975). These mechanical defences appear to have been largely overcome by most recent grass eaters, but only after the evolution of continuous-growth teeth with very hard slicing surfaces and very complex enamel patterns. As shown by Guthrie (1971) for microtine rodents, abrasive diets must have been a most important selective factor in the evolution of grazers' dental patterns. There are many grasses which, in addition to mechanical defences, have evolved chemical defences and are unpalatable to herbivores, and they are consumed less frequently than nontoxic or palatable ones (e.g. Freeland 1974, Bergeron 1980). Furthermore, palatable species growing in close association with unpalatable ones are grazed less heavily than if they grow alone (McNaughton 1978). These facts, among others (McNaughton 1979), point to the existence of a coevolved system in which grass and grazers have undergone stepwise reciprocal adaptations (Janzen 1980a), but do not suggest precisely a mutualistic basis. In relation to secondary compounds, Owen and Wiegert argued in a puzzling sentence that "the variety of secondary compounds in different species of grasses both encourage and limit consumption". Without further elaboration of this semantic paradox, one is forced to remain sceptical towards the argument. Diversity of secondary compounds is not in itself evidence for consumer-resource mutualism if one judges from the cases reported so far from nature (see e.g. Janzen 1980b for a particularly well documented example).

Plant biomass destruction by herbivores depresses reproductive output not only in grasses (McNaughton 1979, Owen and Wiegert 1981, and references therein), but also in other plants (e.g. Rockwood 1973, Janzen 1976, Stephenson 1980) and this fact has selected strongly for defence mechanisms. Grasses have evolved varied responses to biomass destruction, as discussed by Owen and Wiegert (1981) and McNaughton (1976, 1978, 1979), just like plants in other growth forms (Harper 1977, Grime 1979, Rosenthal and Janzen 1979). Predators have selected for recognition patterns among prey animals, based on the accurate perception of shape, colour patterns, or other features unequivocally identifying a predator at the eyes of the prey. For grasses, lacking sensorial and escape abilities, the predator's feature most predictably associated with its presence is the saliva left on the plant *after* feeding. Herbivores must thus have consistently selected for saliva-responsiveness among grasses, in a manner equivalent to birds of prey having selected among avian prey for responsiveness to the image of "short neck and long tail moving in the right direction" (Tinbergen 1969). Rapid detection of defoliation by grazers has some obvious proximate advantages to the plant through (1) replacing the lost photosynthetic machinery before actual metabolic defficiencies may trigger responses; (2) decreasing the chances of colonization by competing species of vacant microsites created by the grazing action (see e.g. Watt 1962, Harper 1977: 455); and (3) providing an opportunity of invading new microsites left vacant after the partial destruction of neighbouring plants. There is thus no particular reason to see grass responses to grazing as a process other than a response having evolved in the context of a highly coevolved predator-prey-like system and one which uses saliva as a proximate cue for predator recognition.

Plant-herbivore systems are enormously intricate and involve many feedback loops operating a both ecological and evolutionary time scales (Janzen 1978, 1979, McNaughton 1979, Coupland 1979, Breymeyer and Van Dyne 1980, Caughley and Lawlor 1981). There is thus ample room for suggesting bizarre higher-order relationships between participating organisms. After all, Why not to consider grass compensatory growth after damage as a sophisticated defensive-aggressive method against grazers? The continuous enrichment of grazing grounds to herbivores could generate a positive feedback having destabilizing effects on herbivore populations, leading to eruptions followed by sudden crashes in herbivore numbers. Then, viable grass seeds in the soil and underground parts still alive could restore grass populations, reproduce and shed seeds prior to the rebuilding of herbivore populations. Mental exercises as this one could lead anyone to suggest further appealing and superficially plausible hypotheses which, unfortunately, would be as unlikely and hardly testable as Owen and Wiegert's one.

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Grasses and grazers: is there a mutualism?

Denis F. Owen, Dept of Biology, Oxford Polytechnic, Headington, Oxford OX3 OBP, England
Richard G. Wiegert, Dept of Zoology, Univ of Georgia, Athens, GA 33602, USA

We welcome these contributions. There is no doubt that our "sweeping generalization" is open to question – that is why the paper was written. The commonly accepted view is that grasses and grasslands suddenly appeared, perhaps because of some change in climate, and then grazers evolved to take advantage of new feeding opportunities. Our view, however, is that there is an intricate coevolved mutualism. Like any other hypothesis, ours cannot be "proved", but there is (in our opinion) sufficient evidence to justify constructing an explanation for the formation of grasslands dominated by perennial grasses that differs from the conventional view. We cite this evidence but make no claim of "proof".

Our paper puts forward a hypothesis requiring a new look at plant-herbivore relationships, this time with reference to grasses and grazers, but always in the context of our more general hypothesis that plant-feeders can, in a variety of ways, increase the relative fitness of the plants they eat (Owen and Wiegert 1976, Owen 1980). There is, we agree, difficulty in measuring relative fitness. Even with the commonly accepted mutualisms between pollinators and flowers and between fruit-eaters and fruit, estimates of relative fitness of the participants are largely lacking.

We found Silvertown's contribution rather superficial. He appears to be astonished at our audacity in suggesting such an outrageous idea, and most of the points he makes seem to us to be trivial. For example, seasonal alteration of diet by grazers is no different from seasonal alteration of flowers visited by pollinators, and we cannot see what bearing this has on the argument. But we have no quarrel with his conclusion that in some species of grass grazing is necessary for survival. This in itself is a priori evidence for mutualism, since few would dispute that the existence of grass is necessary for grazers.

Herrera's contribution is more substantial and is largely a critique of our interpretation of the mouse-sorghum experiment which, as we were careful to point out, was conducted in highly artificial circumstances. Neither this experiment, nor the possibility that any grazer produces saliva which stimulates grass growth, are essential to our hypothesis, and in retrospect we perhaps made a little too much of the idea in our paper. Whether or not there is a saliva effect will doubtless be demonstrated by a more realistic experiment than the one we cite.

In attempting to refute our hypothesis, Herrera invents three polymorphisms: the existence of saliva-responsive and saliva-nonresponsive genets of the same species of grass; long-lived saliva-responsive genets without chemical defences and short-lived saliva-responsive genets with powerful chemical defences; and a population of grazers with individuals that produce saliva that stimulates grass growth and those that do not. We are entertained by this multiplicity of polymorphisms and without denying their existence, suggest that