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## How Important Are Consumer Species to Ecosystem Functioning?

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### SUMMARY

Species-level and ecosystem-level perspectives can often be combined to better understand nature. To date relatively few studies have explicitly combined these two perspectives; however, the insights these studies offer have been impressive. Considering species as embedded in ecosystems and as potentially having feedback effects that can alter ecosystem function is a powerful way of conceptualizing and analyzing ecological systems. Ecosystem-level phenomena constrain the populations and behavior of consumers, and the effects of consumers seem often to be mediated by changes in ecosystem functions such as productivity, nutrient cycling, and nutrient flows across ecosystem boundaries. These changes often are caused by nontrophic as well as trophic activities, and they may involve changes in behavior of plants. Just how commonly particular herbivore species will prove to control ecosystem functioning remains to be tested in many systems, using techniques with adequate power to discriminate ecologically meaningful effects.

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## HOW IMPORTANT ARE CONSUMERS TO ECOSYSTEM FUNCTIONING?

It is relatively easy to find examples where a particular herbivore or higher level consumer has caused significant shifts in species composition, diversity, productivity, decomposition, nutrient cycling, nutrient loss or input, or geomorphic or hydrologic processes (Huntly, 1991). Nevertheless, the generality of consumer effects on ecosystem dynamics is hotly debated. Do most consumers affect the dynamics of their ecosystems and in species-specific ways, or do relatively few consumers have key effects? Are freshwater ecosystems more commonly influenced by herbivores or trophic cascades than are terrestrial or marine? Are grasslands more strongly influenced by herbivores than are forested ecosystems? Do planktonic systems function differently than benthic systems with respect to consumer effects? What proportion of consumer species significantly mold ecosystem function, at what scale, and by what mechanisms?

Here, I review ways in which consumers influence ecosystem processes and ask how significant consumer species are to ecosystem functioning. My focus is on primary consumers; by inference, higher level consumers that alter the behavior and population dynamics of herbivores may have like effects. These "cascading trophic effects" of higher consumers are discussed elsewhere in this volume (e.g., Grimm, Ch. 1; Power, Ch. 6; Estes, Ch. 15; see also Matson and Hunter, 1992). I use the term "consumer" interchangeably with "herbivore" and "primary consumer."

There have been far more studies of effects of consumers at the ecosystem level in aquatic systems than in terrestrial (for instance, Carpenter, 1988, Carpenter et al., 1991). It is not yet clear that the strong effects demonstrated on species composition, productivity, and nutrient dynamics in these systems are not also present or have not historically been present in terrestrial systems as well. Studies of the soil food web have also often focussed on effects of consumers at the ecosystem level (for instance, Ingham et al., 1989 and references therein; Anderson, Ch. 10; Parmelee, Ch. 11; Bengtsson et al., Ch. 16), but the dominant consumers in these food webs are detritivores rather than herbivores.

The most unequivocal evidence that herbivores affect ecosystem processes comes from experimental manipulations of herbivore populations, either directly excluding herbivores or manipulating higher-level consumers that control size or composition of the herbivore trophic level. These experiments have produced some clear demonstrations of large herbivore effects on ecosystem dynamics (for instance, primary productivity and rates of nutrient cycling) in both terrestrial (Cargill and Jefferies, 1984; McNaughton, 1985; Pollock et al.,

Ch. 12) and aquatic (Carpenter, 1986, 1988; Power, 1990c) ecosystems. In many other cases, alteration of ecosystem function was not directly measured but is implied by extensive changes in community structure (Huntly, 1991).

Another approach has been to use statistical techniques to separate effects of consumers from those of other attributes controlling ecosystem function using observational data. Such studies have shown comparably large and independent effects of herbivores and resources (phosphorus in lakes, Carpenter et al., 1991; nitrogen or rainfall in grasslands, McNaughton, 1985) on primary production and producer standing crop.

There are not enough direct tests to infer how often consumers are important, how important they tend to be, or if there are differences among types of ecosystems or herbivores in kind or strength of effects; however, the studies cited previously do indicate that consumers can have a strong influence on ecosystem dynamics. One can argue that biotic and abiotic components of ecosystems should be viewed as an integrative system (Shackak and Jones, Ch. 27), rather than as driven from below by abiotic factors or primary productivity or as driven from above by consumers. McNaughton (1985) has argued this point particularly well; he suggests that "the physical setting controls the bounds of ecosystem development, and biotic evolution and interactions control ecosystem function within these."

### EFFECTS OF ECOSYSTEM STRUCTURE/FUNCTION ON CONSUMERS

The effects of consumers on ecosystem processes commonly are feedback effects. That is, the kinds and numbers of organisms in an ecosystem are fundamentally constrained by various ecosystem-level traits. These limit the number of animals within an environment, and influence their location and activities within it. Both the population density and the behavior of consumers, the way in which they are distributed across and use their habitat, are strongly controlled by ecosystem-level traits.

Most simply, the primary productivity of an ecosystem sets a maximum limit on the population density of consumers that can be supported. This is the basis of Oksanen's and Fretwell's arguments that consumers will strongly limit plant biomass at levels of ecosystem productivity that support high herbivore biomass, but that are not sufficient to support enough carnivores to limit the herbivores (Oksanen et al., 1981).

Variation in primary productivity on a smaller scale also affects the behavior of many herbivores, and thus determines the pattern of their impacts within an area. The degree to which animals concentrate their activities in particular microhabitats is widely appreciated. Work with pocket gophers in

Minnesota has shown that populations, burrow systems, and foraging tunnels all appear to be located in areas of higher than average soil nitrogen, primary productivity, and food availability (Inouye et al., 1987a; Huntly and Inouye, 1988). Price (1992) gives many examples of herbivores, particularly insects, that selectively exploit high-quality resource patches, choosing both among and within individual plants, plant species, and habitat patches. He also poses the interesting hypothesis that eruptive or outbreak species result from population biology that precludes effective resource assessment. If this is the case, it provides a clear example of a species-level trait that translates into a particular pattern of ecosystem-level effects.

Nutritional factors other than productivity or nitrogen availability may similarly affect animal population density and foraging. McNaughton (1988, 1990) has shown that both the spatial location of concentrations of nonmigratory ungulates and the movement patterns of migratory ungulates in the Serengeti are strongly correlated with availability of Na, Mg, and Ca in forage. The historical density and migration patterns of North American ungulates also appear related to mineral availability, particularly Na, Ca, and Mg (Jones and Hanson, 1985). A number of small terrestrial consumers also are reported to be sensitive to differences in mineral availability. In one case, the foraging responses of voles to an experimentally created difference in Na content of vegetation was sufficient to cause local nitrogen enrichment (Inouye et al., 1987b). It is thought that mineral nutrients are not important to diet selection of marine or aquatic herbivores (Lodge, 1991); however, nutrient fractionation and regeneration by consumers can alter which nutrients limit algal productivity (Sturner, Ch. 23).

Other aspects of the environment also constrain both population density and behavior of herbivores. Water sources are foci of animal activities in many terrestrial ecosystems, resulting in greatly altered vegetation and nutrient dynamics. Refugia from predation appear to be a major factor generating pattern in the activities of animals in all sorts of ecosystems (Jefferies and Lawton, 1984). Examples of this include riverine and lacustrine fishes, zooplankton, caterpillars, reef animals such as crabs and fishes, sea urchins, pikas, moose, and numerous other animals that use dens or burrows (Jefferies and Lawton, 1984; Menge et al., 1985; Huntly, 1991).

Habitat fragmentation and isolation also can affect the kinds, numbers, and effects of consumers. Animal species may differ in their abilities to exploit habitat patches of differing size or isolation (Foster and Gaines, 1991). A recent study of tent caterpillar outbreaks in forests in Ontario, Canada, shows that outbreak duration is strongly correlated with forest fragmentation (percent edge) but not with abundance of the primary host plant (Roland, 1993).

The activities of consumers also may be patterned in ways that are largely independent of preexisting patterns of plant resources or the physico-chemical

environment. These too may feed back to alter vegetation, productivity, and nutrient dynamics. For instance, the position of animal trails has been shown to vary predictably with animal size and topography (Reichman and Aitchison, 1981). Social interactions such as territoriality and mate location also affect the spatial distributions of consumers and their impacts.

### HOW DO CONSUMERS AFFECT ECOSYSTEM FUNCTIONING?

Consumers are constrained by the ecosystems they inhabit, but they also are capable of modifying those ecosystems. Consumers eat plants or plant parts, but they also do many other things. Many herbivores clip or tear and waste plant tissues, providing inputs of green litter and detritus. Various herbivores also trample, scrape, or bulldoze plants. In addition consumers affect the physico-chemical environment in a variety of ways. They form trails, nests, mounds, burrows, and wallows; and they move, mix, and structure soils, sediments, and other materials.

Below I distinguish trophic effects, the effects that arise directly or indirectly from removal of biomass by herbivores, from nontrophic effects, those that are caused by other things that herbivores do. Trophic effects are reasonably well dealt with in theory and have been the focus of the majority of studies of herbivores' effects on ecosystems. Nontrophic effects are far less well studied and little theory has been developed for them. Many nontrophic effects are of the sort that Lawton and Jones (Ch. 14) term ecosystem engineering.

I also suggest that herbivores frequently are a cause of spatial and temporal structure in environmental conditions. Both trophic and nontrophic activities contribute to production of structure, which provides opportunities for different sorts of primary producers to persist in communities, often changing species composition, tending to increase diversity, and probably affecting spatial and temporal stability of ecosystem productivity and nutrient dynamics.

#### Trophic Effects

Herbivores clearly often affect the species composition of the plant communities they inhabit (Huntly, 1991). Plant species differ in their growth phenology, maximal growth rates, typical size and allocation patterns, nutrient and water uptake and retention, and litter quality and quantity (Pastor et al., 1993; Wedin, Ch. 24). Thus, herbivores that alter plant community composition should often alter ecosystem dynamics. Moderate grazing frequently produces more productive communities, and high grazing can result in conversion to a much less productive system.

In addition to removing plant biomass, herbivores process that biomass and return fractions of it as feces, frass, urine, or other excretions. These herbivore-mediated chemical conversions can have significant effects on productivity and on the nutrient supply to plants (McNaughton, 1985; Bianchi and Jones, 1991; Huntly, 1991; Sterner, Ch. 23).

Although less often considered, herbivores also may affect the behavior of a plant, that is, they may change the way in which a plant of a particular species functions and interacts with other species or abiotic components of its environment. By using the term "behavior," I intend to point out the conceptual similarities to processes well appreciated for animals with predators: a predator can change the abundance of a prey population and thereby change that species' quantitative effects on other species or ecosystem components but not change the rules describing those interactions. Alternatively, a predator can cause change in the behavior of its prey, change in the way in which it interacts with its environment (Kotler and Holt, 1989; Huntly, 1991). Examples of this include consumer-induced changes in plant chemistry or form that alter the rate or phenology of nutrient, water, or light use or the litter loss characteristics. These changes appear to be very common (Carpenter, 1988; Brown and Gange, 1990; Louda et al., 1990) but have rarely been studied explicitly in the context of consumer effects on ecosystems, particularly for terrestrial ecosystems. Holland et al. (1992) recently modelled this sort of plant behavioral change, focussing on changes in allocation in terrestrial plants, which they concluded may be more important in stimulating productivity of terrestrial systems than the more commonly studied herbivore inputs of dung and urine. Clearly more work is needed on this aspect of herbivore effects on ecosystems.

The effects of herbivores, even when caused by straightforward trophic interactions, may be manifested through landscape-level dynamics. An example may illustrate what I mean by plant behavior being a critical element of herbivore effects on ecosystems, as well as showing the value of landscape-level considerations in what might at first be considered a smaller-scale question. The northern range of Yellowstone National Park is grazed by elk and bison, which currently number roughly 20,000 and 500, respectively. The effects of these large native grazers on their range is of continuing interest, and Frank and McNaughton (1992) recently showed that grazing of grassland sites either increased or did not affect short-term primary productivity. The effects of these migratory grazers, however, have a larger scale context as well (see Turner and O'Neill, Ch. 19). My colleagues R. Inouye, D. Frank, W. Minshall, J. Anderson, and I hypothesize that the exchanges of nutrients between upland grasslands, riparian areas, and streams are affected by the large grazers, which not only graze uplands, but also alter the form and phenology of the dominant riparian vegetation, particularly willows and cottonwoods. The

balance of nutrient flows among these system components should be very important in determining the net effects of consumers on the long-term productivity of the ecosystem they depend on and influence. We are investigating this scenario, which requires constructing nutrient budgets at several spatial scales and at various herbivore densities.

Other sorts of consumers also affect nutrient flows between terrestrial and aquatic ecosystems. Emergence of terrestrial adult forms of insects or amphibians that have aquatic larval forms can provide nutrient transfers (Seale, 1980; Power, Ch. 6), and terrestrial consumers can alter the quantity and quality of litter inputs to streams (e.g., Irons et al., 1991). Consumers that graze or otherwise disrupt aquatic macrophytes can affect fluxes between pelagic, littoral, and shore regions (Carpenter and Lodge, 1986; Carpenter, 1988).

### Nontrophic Effects

Nontrophic effects result from direct effects of consumers on the physico-chemical environment (such as moving and structuring soil, sediment, or other materials; burrowing, forming trails) as well as from their nontrophic effects on plants (trampling; clipping, scraping, or cutting but not eating plants, or otherwise causing greenfall). Although experiments in which herbivores are removed from areas are often interpreted as showing effects of herbivory, these in fact show net effects of herbivores, including all of their activities.

These nontrophic effects, many of which fall into the category that Lawton and Jones (Ch. 14) call "allogenic engineering," are far less well studied than are trophic effects; a preliminary conceptual framework for understanding them is laid out by Jones et al. (1994). Certainly the nontrophic effects of beavers are responsible for a major portion of their influence on ecosystems, although they also forage selectively and alter plant species composition (Pollock et al., Ch. 12). Many consumers may have similarly far-reaching nontrophic effects. Bertness (1984a) suggests that snails such as *Littorina littorea* limit formation of shallow soft-bottom habitat and marshes, as a result of bulldozing sediment while grazing. Numerous consumers influence soils by mounding, mixing, and tunneling, and these affect aeration, water movement, topographic relief, and nutrient dynamics (Hole, 1981). Even such small invertebrates as scarab beetle larvae can move substantial amounts of soil (Kalisz and Stone, 1984). The geomorphology and sediments of marine and aquatic ecosystems are similarly affected by consumers (Huntly, 1991; Levinton, Ch. 3).

Engineering of the physical environment is a bit harder to visualize for planktonic systems, but effects of consumers on macrophytes clearly provide environmental structure that influences planktonic communities via its effects on fish and zooplankton and that may have additional effects via changes in lake

chemical and physical properties (Carpenter and Lodge, 1986; Carpenter, 1988). Phytoplankton intercept light, influencing the light environment, water temperatures, and mixing patterns of marine and fresh waters; and zooplankton produce fecal pellets that may sink and transfer nutrients to deeper aquatic subsystems (Jones et al., 1994). Also, generation of chemical patches may be analogous structural engineering in planktonic systems (Sterner, Ch. 23).

Trophic and nontrophic effects may be intertwined, as in the case of fishes that scrape sediment from algal-covered rocks, thus retaining a more productive community to exploit (Power, 1990c) or of pocket gophers whose mounds maintain annual plants of relatively high productivity and nutrient content in fields and meadows (Huntly and Inouye, 1988). In these cases, the nontrophic effects of animals have potential fitness paybacks in the form of trophic rewards.

### Environmental Structure

Herbivores often, through either trophic or nontrophic pathways, strongly modify the spatial and temporal structure of the environment, and this may be a major overlooked way in which ecosystem function is patterned by consumers (Grimm, Ch. 1). Environments can be viewed as having structure of various sorts: they have spatial patches that differ in their characteristics and a given area may change in its characteristics seasonally and among years. Habitat quality for organisms thus varies in space and time, and the feedback effects of these organisms on ecosystem function will also vary.

Variation in the suitability of habitat patches in space and in time has strong effects on populations and communities. Environmental variation provides opportunities for populations to respond in nonlinear or nonadditive ways that result in species abundance patterns that are not simple averages over habitat conditions (Chesson and Huntly, 1989, 1993). It seems that ecosystem dynamics should also be affected by the sorts of environmental structure that consumers create.

**Disturbance—spatiotemporal structure.** The effects of herbivores in ecosystems have sometimes been conceptualized as disturbance, as herbivores may physically disrupt patches or may consume plants in a patchy fashion. Many of these are among the most conspicuous effects of herbivores, for instance gopher mounds, or trampled areas of high animal activity, or patches scraped clear of algae or sediment. However, consumers produce many less conspicuous sorts of disturbances, and these tend to be overlooked. Vole runways provide a good example of relatively inconspicuous disturbed patches that animals create. Although these are small (typically a few centimeters wide) and disappear quickly in the absence of voles, their effects may be much more significant than their size and longevity would suggest. Ericson et al. (1992)

report that more than 90% of establishment and survival of willow seedlings in a successional field in Sweden occurred in vole runways. Furthermore, establishment was largely limited to years following a vole population peak.

*Spatial structure.* Many environmental characteristics cause herbivore feedbacks resulting in a relatively long-term spatial structure to the environment. Refugia around which animals concentrate their actions provide a common example. Also, less frequently but intensively used areas such as buffalo wallows may provide relatively permanent patches of differing soil and plant characteristics and dynamics. Gopher mounds may differ in soil characteristics from surrounding undisturbed areas and therefore be persistently different patches (Inouye et al., 1987a).

The feeding activities of herbivores may in themselves cause feedback that results in the development of persistently grazed patches of higher productivity than adjacent ungrazed patches within a previously more homogeneous environment. This is reported for a wide variety of consumers, including domestic livestock, native free-ranging ungulates, zooplankton, crayfish, small mammal and insect species, snow geese, fishes, and a number of reef animals (McNaughton, 1985; Bianchi and Jones, 1991; Huntly, 1991).

*Temporal structure.* Many herbivores, both vertebrate and invertebrate, and including marine, freshwater, and terrestrial animals, have large population fluctuations. Both their population lows and their population highs can have lasting effects on ecosystem functioning (see also Pace et al., Ch. 7). Ecologists have sometimes incidentally observed a consumer population high that resulted in a major shift of species composition and presumably ecosystem function (e.g., Berdowsky and Zeilinga, 1987; Noy-Meir, 1988). Forest insects with outbreak population dynamics are known to have these sorts of effects (Schowalter et al., 1986), but in many other cases, the effects were entirely unexpected and the fact that a consumer was responsible for the change in system state would be difficult to infer in retrospect.

Research on blacktailed jackrabbits in Idaho sage-steppe provides an interesting example (A. Porth, N. Huntly, and J. Anderson, unpublished). The population peaked in fall 1992, and, shortly after snowfall, the rabbits disappeared from most areas of our 2,300 km<sup>2</sup> study area. We subsequently located radio-collared animals in an area of several square kilometers in which several thousand rabbits were present. The jackrabbits browsed virtually all sagebrush in this area and attracted high concentrations of predators. Within 2 months, the population had collapsed, and the snow was covered with patches of blood, carcasses, fecal pellets, and urine spots. Animals that had fed and gained weight over a large area of sage-steppe had concentrated and died in a few small areas, resulting in large imports of nitrogen and other nutrients into the concentration areas. Clearly, this phenomenon can rarely be observed, but it may occur com-

monly during the roughly decadal population peaks and could have long-term effects on moderate-scale pattern of vegetation and soil fertility.

In a number of cases, plant species appear to have established only during periods of low herbivore density (Huntly, 1991). Presumably the herbivores are usually sufficient to prevent establishment of seedlings or germlings of these species, but once established, the plants can persist in the face of herbivory and their characteristics affect ecosystem dynamics.

Also, the effects of consumers on ecosystems may depend on particular weather conditions and therefore arise only when both the consumers and the physical conditions are appropriate. Hobbs and Mooney (1991) showed an effect of pocket gophers on vegetation that occurred only with sufficient rainfall, and Dayton (1985) notes effects of weather on both consumers and algal propagules that control establishment vs. demolition of kelp beds. For long-lived plants or plants with long-lived propagules, a small window of time is sufficient to produce lasting effects on their populations and any ecosystem-level effects they may have.

## HOW CAN WE BETTER UNDERSTAND THE IMPORTANCE OF CONSUMERS?

I have discussed ways in which herbivores can significantly influence the structure and function of ecosystems and have suggested that it may be particularly interesting to consider (1) effects of consumers on plant behavior, (2) the influence of consumers at a landscape level, (3) nontrophic effects of consumers, and (4) effects of consumers on ecosystem structure and its consequences to ecosystem processes. The empirical data base is not yet sufficient to resolve when, where, why, and how much consumers matter to ecosystem functioning. The following are practical suggestions for how to obtain better data for answering these questions. These suggestions do not concern only methodology, rather they involve important conceptual issues as well.

### A Long-Term Perspective

Both the physical environment and the population dynamics of species vary over time. Herbivores that are only occasionally abundant, because their dynamics are cyclic, because their abundance depends on certain weather conditions, or because their primary food is only occasionally abundant, may nevertheless have strong and lasting effects on ecosystem function. Agents of successful biological control certainly illustrate this, as do a number of examples cited earlier. Furthermore, the physical environment varies in time due to weather patterns and geomorphic processes, and the life spans of pri-

mary producers and higher-level consumers constrain the rates at which consumer effects can be seen. An appreciation of consumer effects on ecosystem functioning must take this long-term environmental framework into account.

Although all studies cannot be long-term, it is necessary to estimate the probable long-term dynamics of a system. A careful analysis and linkage of organismal biology, the physical environment, and various feedbacks among these may often allow reasonable extrapolation from the shorter-term work we must do to the longer-term context we seek to understand (e.g., Chesson and Huntly, 1989; Likens, 1989; Huntly, 1991). Perhaps the need to understand typical long-term dynamics, rather than simply current function, is an important reason for putting species biology into ecosystem models.

### Comparing Relative Effects

Absolute rate of change is often confused with strength of effect. This is arguably at the root of many disagreements over the importance of consumers in different ecosystems. More productive systems can show larger absolute changes in biomass over a given time interval; they also can show faster responses to a given perturbation. Ecosystems in which the organisms have inherently faster growth rates, such as pelagic systems dominated by phytoplankton, as opposed to meadows or forest, in which the dominant primary producers have life spans of decades and centuries, also can show more rapid changes in species composition and nutrient dynamics. However, more rapid change should not be mistaken for evidence of larger effects. Rather, the relevant response for comparisons of importance of herbivores among ecosystems is proportional to relative change in productivity, nutrient flux, or whatever variable is being compared.

### The Concepts of Power and Effect Size

Statistics are now widely used to guide interpretation of ecological data. Statistical significance levels (for instance,  $P < .05$ ) are expected to be reported in ecological studies, but the arbitrary nature of this statistic is poorly appreciated. In particular, the interrelated concepts of power of a test and effect size are often ignored. The power of a test, the probability of rejecting a false null hypothesis (or detecting a real effect), is a measure of how strong a test is. A very powerful test, one with large sample size relative to the background variation, can detect very small effects. Thus, an effect may be highly statistically significant, but account for a tiny fraction of the variation in the data; it may very well not be ecologically significant. To find no effect is trivial when a test has too little power. Just what effect size is ecologically meaningful is open to differences of opinion, but to consider statistical significance alone, without consideration of power, is to abdicate responsibility for think-

ing about what size effects are ecologically meaningful. These issues apply to interpretations of surveys as well as of experiments and are discussed in detail elsewhere in the ecological literature (e.g., Toft and Shea, 1983; Yoccoz, 1991) and in many experimental design texts (e.g., Winer, 1971; Steele and Torrie, 1980), which present how to calculate such useful things as power of a test, sample size needed to detect an effect of a particular size, or degree to which an effect occurs.

### **Animal Behavior and Ecosystem Effects**

I am continually impressed with the necessity to consider animal behavior when designing schemes for study of animals' influences on the ecosystems they inhabit. Random placement of samples or exclosures is probably rarely the best way to study these systems, because the effects of animals are likely to vary spatially. When animals have effects that vary systematically from place to place, a design in which relevant sorts of habitats or patches are treated as blocks will provide much more power to detect those effects. A good knowledge of species biology informs these sampling decisions.

A study of effects of pikas on vegetation illustrates this concern (Huntly, 1987). The feeding preferences and selectivity of pikas varied predictably along a habitat gradient, distance from talus. Pikas grazed more heavily but less selectively near talus. Exclosures that were blocked with respect to distance from talus demonstrated that pikas significantly affected vegetation in the area adjoining talus. However, because the animals had different effects at different locations, an analysis of all exclosures pooled would not detect those effects, which effectively cancelled each other out in the pooled data.

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