Benefits of Group Living

Here is a list of possible benefits of group living. Keep in mind that, even if we see that an advantage is currently operating, it may not have led to the evolution of sociality in any particular case; rather, it may be a secondary benefit appearing after sociality had already evolved. Also remember that these are not mutually exclusive.

1. **Protection from physical factors.** Abiotic factors, especially cold, rainy, or snowy weather, can promote grouping. For example, bobwhite quail (*Colinus virginianus*) survive low temperatures better when grouped than when isolated (Gerstell 1939). Gregarious butterfly larvae (*Aglais urticae* and *Inachis io*) experience a less variable range of body temperatures than do solitary larvae (*Polygonia calbum* and *Vanessa atalanta*, Bryant et al. 2000). This benefit would result in aggregations, but not necessarily organized social groups.

2. **Protection against predators.** One of the most often documented selective advantages of living in a group is protection against predators. As discussed in chapter 15, there are several mechanisms by which animals can avoid predation by being in a group. To illustrate and reinforce these points, we'll look at a nicely worked-out example on a spider we've met before, *Metepeira incrassata*, studied by Uetz and his colleagues (reviewed in Uetz and Hieber 1997). This is a colonial spider that has a shared frame web to which all spiders contribute silk. Within that frame web, each individual spider builds its own orb web, which it defends from others (figure 19.1*a*). Spiders are attacked by wasps and hummingbirds. Being in a colony, as opposed to being alone, benefits an individual in several ways. First is the encounter effect, which affects the probability that a predator locates a colony. This relationship is somewhat complex: as colony size increases, the rate that colonies encounter predators also increases. However, the rate does not increase as quickly as expected (figure 19.1*b*), probably because of the apparency of the colonies to predators. A colony of 1,000 spiders is not twice as visible to a potential predator as is a colony with 500 spiders, because some of the spiders are hidden behind others.

   The second factor that reduces predation risk for these spiders is the dilution effect, which reduces individual risk once a colony is encountered. This, as we discussed in chapter 15, is simply safety in numbers: if a predator is going to eat only one prey, it is better to be in a large group than alone. In *Metepeira*, wasps sometimes attack more than one spider in a colony, which reduces the dilution effect. On the other hand, spiders are informed about the presence of a predator through vibrations transmitted through the web, and this early warning effect reduces the capture success of wasps. Overall, there is a decrease in risk with increasing group size that is even steeper than predicted by numerical dilution (figure 19.1*c*).

   Position effects within a colony are also important. Recall Hamilton's (1971) selfish herd (chapter 15): when frogs aggregate to avoid a water snake, it is in each frog's best interest to be in the center of the group. Similarly, spiders on the inside of a colony have reduced risk of predation because they are surrounded by conspecifics, but the trade-off is a reduction in food supply as insect prey are also unlikely to make it to the core (Rayor and Uetz 1990, 1993).

   Young are often especially vulnerable to predators, and in many species group living appears to be an adaptation to protect them. For example, a female "parent bug," a species of Hemipteran (*Elasmucha grisea*), defends her clutch of eggs and developing nymphs by covering them with her body and showing aggressive behavior toward disturbances. Sometimes two parent bugs guard their eggs side by side on a leaf. Mappes et al. (1995) studied whether pairs of females were more effective at guarding their offspring by experimentally constructing pairs of females with clutches by cutting off pieces of leaves with eggs attached and placing them near existing clutches. (By experimentally creating pairs instead of using natural pairs, the researchers could control for any differences between solitary and paired bugs in their guarding efficiency.) Jointly guarding females lost fewer eggs to predators than did single females.

   Predator protection in groups has been shown for herds of ungulates, flocks of birds, colonial mammals, and schools of fish, among others. However, while the mechanisms described here might explain some aggregations, more is required to explain systems where individuals cooperate.

3. **Assembly of sexual species for finding mates.** Solitary sexual species may expend considerable time and energy in simply locating a potential mate. Group-living animals can often find a mate more readily than can solitary species. Some species group together specifically for reproduction; for example, mating swarms are common in insects and in some vertebrates (see chapter 18).

4. **Locating and procuring food.** As we discussed in chapter 15, animals in groups may have better foraging success than solitary animals. We discussed information sharing, where animals learn about the location of food sources. A related advantage is created by tradition; knowledge about resource location can be transmitted to subsequent generations, as it is in sheep (*Ovis canadensis*) (Geist 1971) (see also chapter 14). Animals also participate in cooperative hunting, resulting in increased capture rates and capture of larger prey. For example, Harris' hawks (*Parabuteo unicinctus*) form hunting parties of two to six in the non-breeding season and cooperate to capture rabbits several times larger than themselves (figure 19.2) (Bednarz 1988).

5. **Resource defense against conspecifics or competing species.** Many examples of group territoriality are included here. Among invertebrates, large colonies may have a competitive advantage over smaller groups. The bryozoan *Bugula turrita* occurs in dense colonies on pilings and rocks in shallow water along the coasts of North America. Another species, *Schizoporella errata*, frequently overgrows them, unless the *B. turrita* larvae group together. The resulting dense colonies are less likely to be overgrown by *S. errata* (Buss 1981).

6. **Division of labor among specialists.** In some societies, different individuals have different tasks. This is especially pronounced in the castes of insects such as ants, wasps, bees, and termites. We will discuss this in more detail in the section "Eusociality" later in the chapter.

7. **Richer learning environment for young.** Some species, especially many mammals (primates in particular) depend on learning. Learning provides great plasticity but requires a long period of physiological and psychological dependence on others. Consider hyenas. As we saw in chapter 15, hyenas are highly social species that cooperatively attack prey. In fact, they can learn about which prey are palatable from one another. Yoerg (1991) trained hyenas to avoid a particular type of food (corned beef hash or one of two flavors of cat food) by lacing it with lithium chloride. When trained hyenas were allowed the chance to join with others in eating the same type of food, they overcame their aversion and joined in, demonstrating the importance of social interactions in diet choice for this species.

8. **Aiding (or receiving aid from) offspring or other relatives.** As we will see in more detail later in the chapter, living with relatives gives animals the opportunity to pass on their genes either by improving the chances of success of their offspring or by helping other relatives.

9. **Modifying their environment.** Many species build structures, such as nests, burrow systems, dams, etc. In many cases,

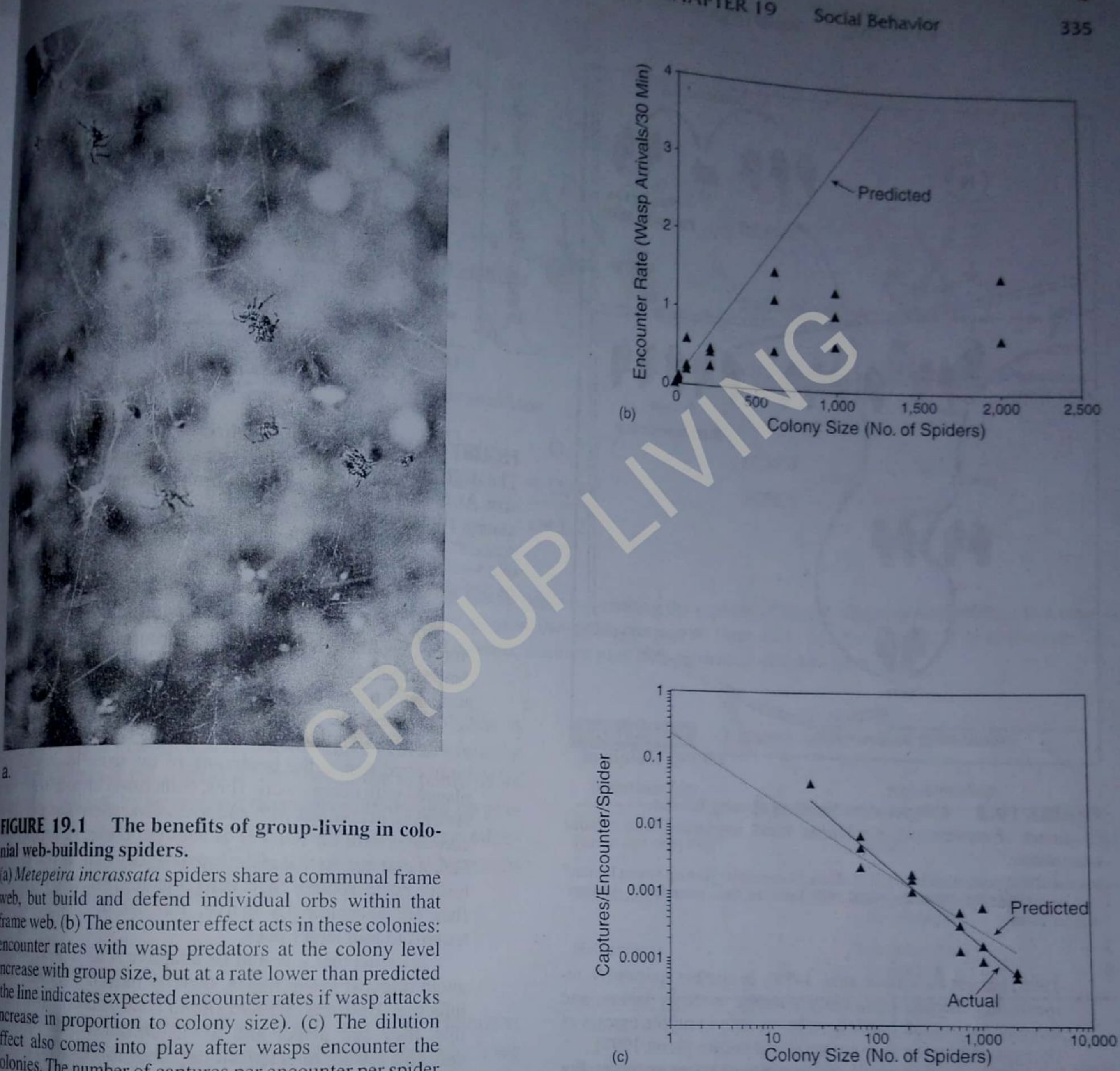

FIGURE 19.1 The benefits of group-living in colonial web-building spiders.
(a) *Metepeira incrassata* spiders share a communal frame web, but build and defend individual orbs within that frame web. (b) The encounter effect acts in these colonies: encounter rates with wasp predators at the colony level increase with group size, but at a rate lower than predicted (the line indicates expected encounter rates if wasp attacks increase in proportion to colony size). (c) The dilution effect also comes into play after wasps encounter the colonies. The number of captures per encounter per spider decrease with colony size even more rapidly than predicted (dashed line is predicted line).
Fig. 1a. Source: Courtesy G. W. Vetz.
Fig. 1b–c. Modified from Vetz, G. W. and C. S. Hieber. 1997. Colonial web-building spiders: balancing the costs and benefits of group-living. In *The Evolution of Social Behavior in Insects and Arachnids*, ed. J. C. Choe and B. J. Crespi, 458–475. Cambridge: Cambridge University Press.

a group can accomplish what a single individual may not. For example, honeybees not only build elaborate nests together, but can actively cool them by fanning, or warm them with microvibrations of their powerful wing muscles (Seeley 1993).

Costs of Group Living

1. **Increased competition for resources.** Conspecifics are likely to have the same resource requirements, so competition for food, shelter, and mates is likely. For example, in prairie dog colonies (*Cynomys* spp.), the amount of agonistic behavior per individual increases as a function of group size. Black-tailed prairie dogs are more highly social and have higher rates of aggression than do the less social white-tails (Hoogland 1979a).

Burying beetles (*Nicrophorus* sp.) compete for an unusual resource: carcasses. Adult beetles prepare a carcass by removing its hair and rolling it into a ball as they bury it, and depositing anal secretions upon it that affect its decomposition. Females lay eggs near a prepared carcass and the larvae make their way to it, where they feed upon it as well as on liquefied carrion regurgitated by adults. Adults sometimes share carcasses and rear their offspring together. In four different species of burying beetles, the total number of larvae per female declines when a carcass is shared (reviewed in Trumbo and Fiore 1994), demonstrating the effect of competition. So why do beetles share? In some species (such as *N. defodiens*), the probability that the nest fails altogether is quite high, so the first adult to arrive at a carcass might be better off to tolerate a newcomer rather than fighting for a resource that is of low value (Trumbo

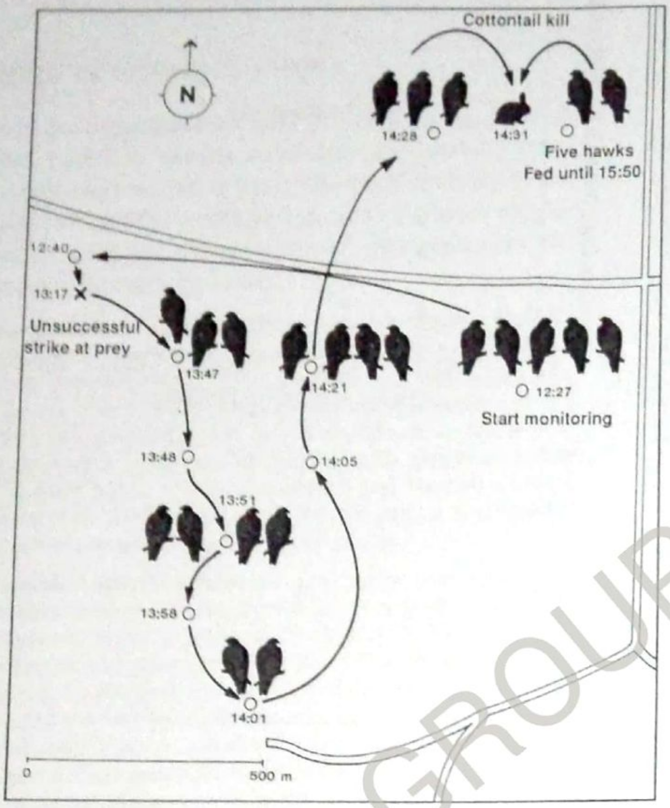

FIGURE 19.2 Cooperative hunting among hawks.
Sequence of movements of a Harris' hawk implanted with a radio transmitter.

Reprinted with permission from J. C. Bednarz, "Cooperative Hunting Among Hawks." in *Science*, 239:1526, 1988. Copyright 1988 American Association for the Advancement of Science.

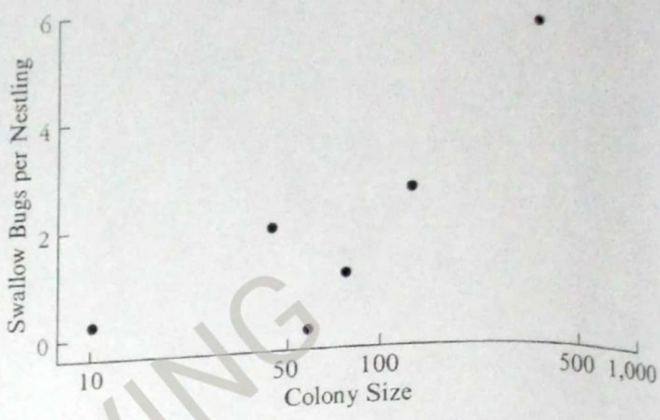

FIGURE 19.3 A cost of sociality.
The degree of parasitism by bugs as a function of swallow colony size. As colony size increases, so does the extent of bug infestation among 10-day-old nestlings.

Source: C. R. Brown and M. B. Brown, "Ectoparasitism as a Cost of Coloniality in Cliff Swallows *(Hirunda pyrrhonata)*," in *Ecology*, 67:1206–18. Copyright © 1967 by the Ecological Society of America, Tempe, AZ.

1995; but see Robertson et al. 1998). In another species (*N. tomentosus*), beetles commonly compete with fly larvae, and three or more adult beetles are better able to rid the carcass of fly eggs and larvae than are smaller numbers (Scott 1997).

Costs of competition may vary across group members. For example, the long-legged web-building spider *Holocnemus pluchei* is facultatively group living; sometimes it lives alone and sometimes it shares a web with conspecifics. When an insect hits the web, spiders charge toward it and will fight vigorously for it, sometimes to the death. The largest spider in the web nearly always wins, so the effect of competition is much more pronounced for small individuals. Nonetheless, many small spiders live in groups, probably in part to save the energetic costs of building their own webs (Jakob 1991).

2. **Increased chance of spread of diseases and parasites.** The correlation between the risk of infection and living in groups has now been well documented. Ectoparasites such as fleas and lice are more numerous in larger and denser prairie dog (*Cynomys* spp.) colonies than in smaller ones (Hoogland 1979a). This is not trivial, as fleas transmit bubonic plague; plague epidemics periodically decimate prairie dog colonies, so members of dense colonies are at risk. Similarly, as cliff swallow (*Hirundo pyrrhonota*) nesting colony size increases, the number of blood-sucking swallow bugs per nest also increases. Cliff swallow nestlings in parasitized nests lose weight and suffer higher mortality than do those in parasite-free nests (Brown and Brown 1986) (figure 19.3).

Sometimes animals battle both internal and ectoparasites. Rubenstein and Hohmann (1989) studied feral horses and parasitic infections on the barrier island of Shackleford Banks, North Carolina. Horses in larger groups have a higher incidence of infection with internal parasites, as indicated by the number of parasite eggs in their feces. As in the prairie dogs and swallows, infection has serious implications: the intensity of infection at the end of one breeding season correlates with body condition at the beginning of the next. Horses are also plagued with ectoparasitic flies, sometimes up to 200 at a time. However, in contrast with endoparasites, group size negatively correlates with the number of flies per horse. Rubenstein and Hohmann suggest that endoparasites play a larger role in structuring horse society than ectoparasites, because even when flies are exceptionally active, females do not leave small harems to join larger ones.

It seems that it would be adaptive if an individual could avoid infected group mates, thereby reducing its own risk of infection. Bullfrog tadpoles (*Rana catesbeiana*) can in fact do this: they can detect and avoid chemical cues from conspecifics that are infected with a pathogen (*Candida humicola*) (Kiesecker et al. 1999).

Although it makes sense that risk of disease should increase with group size, this is not always true. Bluegill sunfish that nest in colonies are less likely to lose their eggs to fungus than are solitary nesters; one likely explanation is that solitary males spend more time chasing predators and less time fanning their eggs, which reduces disease (Côte and Gross 1993).

3. **Interference with reproduction, such as killing of young by nonparents.** For example, when male lions take over a pride, they almost invariably kill small cubs (Pusey and Packer 1987) (see chapter 14). Mexican jays often interfere in the nest of another, stealing nest lining or even destroying the nest (Brown and Brown 1990). Proximity to conspecifics can also increase the risk of cuckoldry, brood parasitism, or sexual harassment.

THE EVOLUTION OF COOPERATION AND ALTRUISM

Group living often has direct fitness benefits for each individual, as we have seen; for example, an animal might be more likely to survive winter weather if it is in an aggregation rather than alone. In cases like these, the evolution of