

4 The Sociobiology of Domestication

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Farming, whereby one organism cultivates a population of another organism, is usually associated with tending of livestock and crop plants by humans. However, similar behavior exists in other organisms, and those examples predate human agriculture by millions of years. The best-known examples of nonhuman farming are the fungus-farming insects (Mueller et al. 2005). In this chapter we use a broader concept of farming, including mutualistic host-symbiont relationships in general, and ask how useful this concept is for analyzing their evolution.

The host in a mutualistic host-symbiont interaction has the same interest as a farmer who cultivates a field of rice or breeds a herd of cattle—namely, maximizing the productivity of its domesticates. Simply put, farmers can be considered as hosts and their crops and livestock as symbionts. Collective performance of the symbionts usually depends on cooperation (Frank 1996). However, within a group of symbionts a “tragedy of the commons” (Hardin 1968) may occur: individuals within the herd may increase their relative fitness within the group at the cost of collective herd productivity (see chapter 3, this volume). This is a fundamental problem of social evolution in a wide variety of biological (and socioeconomic) interactions, ranging from the eukaryotic cell with thousands of mitochondrial genomes, to natural populations of plants or animals, to the farmer with thousands of livestock. Because of the difference in numbers between partners, *domestication*, defined as the genetic modification of one species by another in ways that benefit the modifying species but that would reduce the fitness of the modified species in its original niche, is essentially a process of social evolution. How is lower-level competition within the herd prevented from disrupting collective performance, and thus herd productivity?

First, we review the data from a variety of natural host-symbiont interactions and identify key mechanisms that hosts use to enforce sociality in their livestock. Second, we consider human agriculture and husbandry and identify parallels with nonhuman host-symbiont interactions. We also identify examples of conscious or unconscious group selection of domesticated species by farmers and of unwanted consequences of selection at the level of the individual. Third, we identify opportunities for group selection. While the conditions for selection for cooperation in nature are highly specific and rare, humans can create those conditions in their selection programs and be inspired by natural examples of host-symbiont interactions. Explicitly considering social effects in artificial selection is

a relatively unexplored and potentially extremely important category of improvement of crops and livestock, not only for higher yields but also for greater product quality and, in husbandry, animal welfare.

Is the Distinction between a “Host” and a “Symbiont” Useful?

Many symbioses are asymmetrical, consisting of a large host and smaller symbiotic organisms (Frank 1997). The host can be a multicellular individual with gut bacteria; a eukaryotic cell with intracellular symbionts; a farmer with crops; or a colony itself, such as a colony of social insects that cultivate fungal symbionts. There are various possible criteria for distinguishing the host from the symbionts (table 4.1). In this chapter, we argue that a useful criterion is based on a difference in numbers. Almost invariably, a mutualistic entity consists of a single host individual or an “organism” at a different level in the biological hierarchy, and a group of symbionts. We define “organism” as a relatively conflict-free entity in the biological hierarchy (Queller and Strassmann 2009); for example, an organism can be a single individual or a colony of individuals founded by a singly mated ant queen or a monogamous pair of termite reproductives. Distinguishing host and symbiont based on the number criterion allows us to explicitly consider the significance of cooperation between members of one partner species, the symbionts, and how the other partner, the host, can influence that.

Mechanisms Whereby a Host Maximizes “Symbiont Productivity”

Identified mechanisms whereby a host maximizes “symbiont productivity” can be placed in three main categories (table 4.2): (1) mechanisms that facilitate kin selection; (2) mechanisms that reduce correlation between competitive success of symbionts and reproductive success; and (3) mechanisms that favor competitiveness. All three are based on the assumption that the host organism profits from the collective performance of the symbionts, but they differ in the assumptions they make about the relationship between collective performance of the symbionts and their competitive traits. The first two assume that individual competitiveness of symbionts negatively correlates with collective performance, while the third is the exceptional case in that the host has an interest in competitive traits.

Table 4.1

Differences between host and symbiont

Differences in “power” (Frank 1997). The host is often envisaged as being the partner in control, although this is partially due to an anthropocentric perspective.

Differences in the generation times, with the symbionts generally having multiple generations per host generation, leading to a difference in evolutionary rate. In animal husbandry, the difference in generation time has further dramatically increased due to modern techniques such as embryo transplantation, artificial insemination, and cloning.

(Potential) differences in evolutionary rate. A difference in the generation times potentially results in a higher rate of evolution of the symbionts (but see Bergstrom and Lachmann 2003).

Differences in being external (the host) or internal—that is to say protected from the external environment (the symbionts) or otherwise compartmentalized (Law and Lewis 1983).

Differences in the frequency of sex, with symbionts typically having reduced frequency of sex (Law and Lewis 1983). The examples discussed by Law and Lewis (1983), such as between algae and fungi in lichens and between arbuscular mycorrhizal fungi and plants, provide support for this idea.

Table 4.2

The three main categories of mechanisms whereby a host maximizes “symbiont productivity”

1. Facilitating kin selection		
<i>Indirect</i>	Control symbiont reproduction (vertical uniparental transmission, with bottleneck)	Fungus-farming ants, eukaryotic cells (chloroplasts, mitochondria), some fungus-farming termites
<i>Direct</i>	Control symbiont genetic variation (“weeding”)	Fungus-farming ants (Howe, Schiøtt, and Boomsma 2019), fungus-farming termites (Aanen et al. 2009), fig trees for their mutualistic wasps (Frank 1996; Herre 1985)
2. Reducing correlation between symbiont competitive abilities and reproductive success		
<i>Indirect</i>	Early split reproductive and “somatic” symbionts	“Germline” bacteria that remain quiescent until new eggs are formed, and “somatic bacteria” that provide benefits in sucking lice (Buchner 1965); some rhizobia (Denison 2012); modern human agriculture (germline provided by seed companies or breeding companies)
	Randomize chances to be transmitted analogously to meiosis	<i>Not known to us</i>
<i>Direct</i>	Sanctioning “bad” symbionts	<i>Rhizobia</i> and legumes (Kiers et al. 2003); arbuscular mycorrhiza (Kiers et al. 2011)
	Choice of “good” symbionts.	Squids and luminescent bacteria (Koropatnick et al. 2004; Sachs et al. 2004); artificial selection in human agriculture
3. Favoring competitiveness		
	When the competitive trait is the trait exploited by the host, also known as <i>desirable tragedies</i> (Anten and Vermeulen 2016)	Bacteria that produce antibiotics (Scheuring and Yu, 2012); in human agriculture, e.g., production of timber or large/abundant flowers, breeding of fighting animals

Below we will explain these categories and provide examples. In table 4.2, an overview of the three categories and subcategories and examples of each are provided.

Facilitating Kin Selection

The first means for improving symbiont productivity is by facilitating kin selection. Hamilton’s (1964a, 1964b) rule ($rB - C > 0$) has three parameters: the extra number of offspring in social partners due to a social behavior (the benefit, B), the reduced number of offspring of the individual performing the behavior (the cost, C), and the relatedness (r) between the individual performing and the individual receiving the social behavior. Increasing relatedness among symbionts will increase the indirect fitness component of inclusive fitness (chapter 5, this volume). In many symbioses, symbiont relatedness is an indirect consequence of symbiont transmission. For example, many endosymbionts are transmitted vertically and uniparentally, usually via the egg cell. Uniparental transmission is also usually associated with a bottleneck, so that individuals start with limited genetic variation. For mitochondrial evolution, it has been suggested that uniparental transmission is an important means to reduce the scope for competitive traits that have “virulent” consequences for host fitness (Cosmides and Tooby 1981; Frank 1996). While vertical uniparental transmission is most strict in endosymbioses, this transmission mode also occurs in

some other host-symbiont interactions such as the fungus-farming ants and two groups of fungus-growing termites. Of note is that vertical transmission in the two independent groups of fungus-growing termites is uniparental in both cases, but by different sexes (Johnson et al. 1981; Nobre et al. 2011). In all studied species of the genus *Microtermes*, female alates transmit the fungus to newly founded colonies, but in the species *Macrotermes bellicosus*, males do (Nobre et al. 2011).

Symbiont relatedness can also be manipulated directly by the host. For example, colonies of most species of fungus-growing termites do not regularly have vertical uniparental transmission, except for the two groups just mentioned (Korb and Aanen 2003). Instead, most species rely on horizontal symbiont acquisition via sexual spores in the environment, produced by mushrooms from termite colonies. Even though this would give ample opportunity for mixed cultures, all colonies examined so far are associated with a single fungal clone (Aanen et al. 2009). It has been shown that termites achieve a monoculture even when started from a mixture of strains, because the most common strain achieves more cooperative interactions and produces a disproportionate number of asexual spores that are used to inoculate new fragments of the fungus garden (Aanen et al. 2009; Bastiaans et al. 2015). Also, in the fungus-growing ants, where vertical uniparental transmission is the default transmission mode, frequent horizontal transmission occurs (Howe, Schiøtt, and Boomsma 2019), and mechanisms exist whereby symbiont diversity is reduced (Poulsen and Boomsma 2005). Another example wherein a host enforces high symbiont relatedness are leguminous plants, which carry nitrogen-fixing rhizobial bacteria in root nodules. Each nodule is colonized by a single bacterium, so that relatedness among bacteria of a single nodule is maximal. This organization of genetic variation among groups of bacteria allows plants to effectively discriminate nodules and to sanction unproductive rhizobial strains (Kiers et al. 2003; discussed further below). Finally, fig trees have an interesting pollination mutualism with fig wasps, in which fig wasps lay eggs in fig flowers, and the emerging fig wasps disperse pollen to other plants. Since mating between newly emerged wasps occurs inside the fig, and since males die upon mating, males do not disperse pollen. Each male consumes a seed, however, and thus represents a virulent trait from the fig tree's perspective. Since there is local mate competition, fig wasps adjust the sex ratio depending on the number of foundresses. With a single foundress the sex ratio is female biased, while the proportion of males increases with additional foundresses (Herre 1985). It is thus in the interest of a fig tree to minimize the number of foundresses per flower, and it has been demonstrated that a fig inflorescence is sealed off within 24 hours after colonization, thus limiting the chance of additional foundresses (Frank 1996; Herre 1985).

Steve Frank (1996) has pointed out that there is an important distinction between the direct effect of increased symbiont relatedness on collective performance and the indirect effect due to kin selection facilitated by high symbiont relatedness. An important question is whether symbiont mixing has an immediately negative effect on collective performance—that is, whether competitiveness is induced upon mixing, or whether it is an evolved obligate characteristic because of an evolutionary history of individual selection. For fungi associated with fungus-growing social insects, it has been found that the effect of symbiont mixing is induced upon mixing (Aanen et al. 2009; Poulsen and Boomsma 2005). It has also been shown that there is a direct benefit of “monoculture” of mitochondria for mice

(Sharpley et al. 2012). The same question can be asked for plant communities in human agriculture. Are competitive traits constitutive or induced upon recognition of unrelated individuals, either of the same species or of different species?

Reducing Correlation between Symbiont Competitive Abilities and Reproductive Success

Next to kin selection, repression of competition is the second main cornerstone for the evolution of cooperation (Frank 2003). When opportunities for competition against neighbors are limited within groups, individuals can increase their own success only by enhancing the efficiency and productivity of their group. Therefore, characters that repress competition within groups promote cooperation and enhance group success (Frank 2003). Repression of competition can indirectly lead to more cooperative traits by favoring selection of cooperative individuals or directly, for example, by partner choice or sanctioning. An example of the indirect selection for more cooperative traits is an early split between reproductive and “somatic” symbionts. A nice example is provided by a particular group of gut symbionts of sucking lice. Those symbionts are divided at an early developmental stage into “germline” bacteria, which remain quiescent until new eggs are formed, and “somatic bacteria,” which provide nutritional benefits to the lice (Buchner 1965; see figure 4.1). Since the somatic bacteria are an evolutionary dead end, their only way to increase

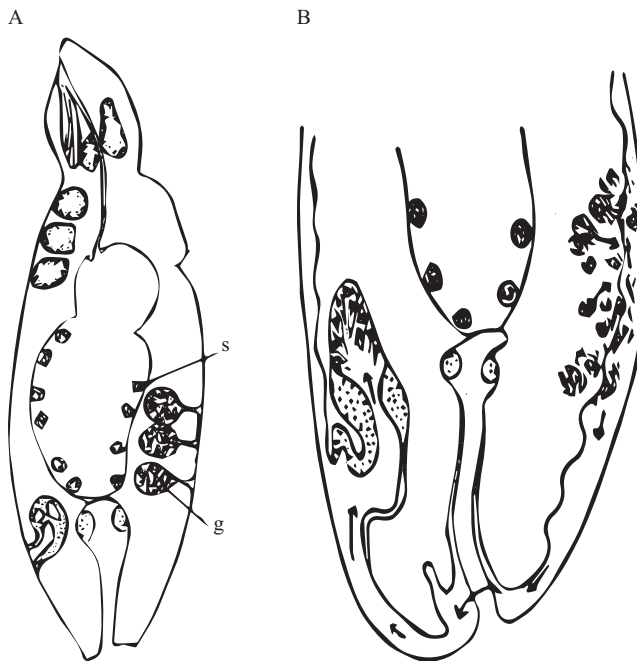


Figure 4.1

The early sequestration of symbionts into germ and soma in the sucking louse (*Haematopinus suis*; redrawn based on Buchner 1965). (A) The symbionts are separated at an early developmental stage into a somatic (*s*) and a germline (*g*) population. The somatic population is contained in storage organs lining the gut, and the germline population is temporarily stored in special organs. (B) Germ-line storage organs degenerate and symbionts are released and flow toward the developing ovaries. The direction of movement is indicated by the arrows.

in fitness is indirectly, by maximizing host benefit, which increases the chance of survival of their genetically related germline symbionts. This example is analogous to the early soma-germline sequestration between cells found in metazoa. There is a nice analogy here with modern agriculture: the seeds of most crops are produced separately from those used in production fields by specialized seed companies. Similarly, in many livestock species, individuals are produced by specialized breeding companies.

An example of direct selection of cooperative individuals is the sanctioning of “bad” symbionts, or the choosing of “good” symbionts. For example, for the earlier mentioned leguminous plants, which live in symbiosis with nitrogen-fixing rhizobial bacteria, it has been found that nonproductive strains can be sanctioned by providing them with less carbohydrates relative to productive strains (Kiers et al. 2003). A similar mechanism has been found in arbuscular mycorrhiza (Kiers et al. 2011). Partner choice has been found in squids and their luminescent symbiotic bacteria (Koropatnick et al. 2004; Sachs et al. 2004). Those bacteria are housed in a special light organ, which probably functions as a camouflage organ that disguises them from predators that swim below the squid. Symbionts are acquired horizontally, not only when squids emerge from the egg, but also continuously throughout their lives. Each day 95% of the symbiotic bacteria are expelled and renewed by horizontal acquisition from the environment. A mechanism has been hypothesized for how the host can choose specific partners based on their luciferase activity. The high concentration of peroxidase produced in crypts of the squid light organs are poisonous (Visick and McFall-Ngai 2000). This poison may act specifically against nonluminescent strains. Because the functioning bacterial luciferase has a higher binding affinity for oxygen than for the peroxidases, luminous strains may escape the effects of the deadly poison (Visick and McFall-Ngai 2000). There is a direct analogy here with modern human agriculture: humans artificially select and have selected their various crops and pets. The question is whether the selection criteria can be improved if group productivity is explicitly taken into account.

Favoring Competitiveness

The above sections show that competition between symbionts often negatively affects performance (e.g., yield) at the group level. An exception to the general rule that competitiveness conflicts with host interest is when the competitive trait is exploited by the host. An example is bacteria that produce antibiotics, which have been found in several insects (Currie et al. 1999; Kaltentpoth et al. 2005; Scheuring and Yu 2012; Visser et al. 2012). More generally, if a host has the ability to recognize desirable characteristics and to select for them, competitive traits can be the target of selection. For example, within eukaryotic cells, mitochondria are tested for functionality on an individual basis by alternation between fusion and fission (Kowald and Kirkwood 2011).

Analogies with Human Agriculture

Competitive Traits in Plants: Examples of and Opportunities for Group Selection

From an agricultural perspective, maximum population-level performance is generally the objective. That is, farmers tend to want to maximize the yield or resource-use efficiency of a crop field or herd of farm animals. If maximization of functions such as seed production

or resource-use efficiency is the objective, then naturally evolved competitive traits resulting in tragedies of the commons (TOCs) are undesirable. Here we discuss examples of such traits, with regard to plants and their relation to crops and with regard to animal breeding. We then discuss how lessons for breeding can be drawn from knowledge of the existence of TOC phenomena.

The most-studied competitive trait in plants is plant height. Height growth involves costs. This is first because taller structures require stronger support structures (McMahon 1973), and taller plants thus have a higher fractional allocation of resources to stems and branches and a smaller allocation to leaves (Stutzel, Charles-Edwards, and Beech 1988). Second, in trees there are hydraulic limitations to height caused by increased resistance in longer transport vessels and increased gravitational potential opposing the ascent of water. Consequently, leaf stomatal conductance and photosynthesis become constrained in tall trees (Ryan, Phillips, and Bond 2006). Thus, a population of relatively short plants has more energy to invest in fitness-enhancing functions such as seed production. However, such vegetation would not be evolutionarily stable as it could be invaded by mutant plants that are taller and thus shade their neighbors.

Many other similarly competitive traits with the potential to produce TOCs exist in plants. For instance, it is known that plants may produce extra roots in the presence of non-self neighbors at the expense of shoot and seed production (Gersani et al. 2001; but see Chen et al. 2015). Leaf area indices of both crop and natural vegetation stands have been found to be larger than values that would maximize whole-canopy carbon gain, because populations with optimal leaf areas for maximal community performance are prone to invasion by plants with larger leaf areas that capture more light (Anten and During 2011). Horizontal leaf angles may have evolved similarly. Vertical leaves favor a better light distribution in the canopy and may thus favor whole-stand canopy photosynthesis, but horizontal leaves are more efficient in competition (Hikosaka and Hirose 1997). The traits mentioned so far relate to physical resource acquisition, but reproductive traits may also have evolved in a similar way. For instance, plants invest energy in fruits or flowers to attract dispersers or pollinators, and there is probably an optimal size of these organs that maximizes visibility of these structures per unit of invested energy. However, if one individual produces more or bigger fruits or flowers, it may become more attractive to dispersers/pollinators and thus attract a bigger share of them (Anten and Vermeulen 2016).

Competitive Traits in Animals: Examples of and Opportunities for Group Selection

In animal breeding there are opportunities for maximizing group performance by breeding for indirect genetic effects (Bijma and Wade 2008). Bill Muir (1996) was the first to state in the literature that selection schemes should therefore take the social aspect into account. Classical, individual-level selection for survival paradoxically led to a decrease in survival because the individuals surviving were the most competitive, that is to say aggressive, ones. Selecting at the level of the family group, in contrast, favored less aggressive, more social individuals. In this way, a fast response to selection against mortality and increased longevity was achieved (Muir 1996). Similarly, in other domesticated animals increases in yield may be achieved by selecting for more social behaviors. For example, a regular practice in dairy farming is the removal of the horns of cattle to prevent them from harmful fighting. Horns are an individually selected competitive trait that decreases group productivity,

and hornless breeds have been selected to increase group productivity. Likewise, in poultry, the beaks of chicken are trimmed. Recent work by Piter Bijma (Bijma and Wade 2008) and others (Muir 1996; Denison 2012) shows that selection for sociality can work.

What Can Crop Breeding Learn from Other Host-Symbiont Interactions?

Given the aforementioned conflict between individual-based selection in many natural settings and the inherent focus on group performance in agriculture, we may reasonably ask what steps have (possibly unwittingly) been made in selecting for increased group performance and what lessons can be learned for the future.

One of the great advances in crop breeding has been the green revolution, which involved strong reductions in plant height in several of our major crops (Khush 1999). The main advantage derived was reduced investment in stem tissue, which allows greater investment in seeds and a smaller chance of lodging (plants buckling, usually due to wind forces or under their own weight). In many fruit crops, grafting is an interesting technique whereby shoots of less competitive and highly productive genotypes can be connected to stem and root systems of more competitive genotypes (Bulley et al. 2005). But probably a broader set of traits has been similarly optimized in crop breeding. When plants were grown at high population density, yields were twice as high in maize varieties released in the 1990s as in varieties released in the 1930s, but there was no difference at low density. These patterns were associated with trait values that run counter to those that produce a TOC: more vertical leaves, smaller investment in male flowers, and slower leaf senescence in more recent varieties (Duvick and Cassman 1999). In another study higher yields in cotton were associated with smaller leaf area (Lu et al. 1994). It has also been documented that modern high-yield varieties produce fewer roots or roots with less competitive architectures than older varieties (York et al. 2015). Together, these findings indicate that crop breeding has, albeit unwittingly, been successful in selecting for traits that run counter to the expression of a TOC and that this development has contributed to significant increases in crop production.

This raises the question of whether further improvements in breeding along these lines are possible, as advocated by several researchers (e.g., Weiner et al. 2010; Denison 2011, 2012). Root traits may provide an interesting avenue. While, as noted, there is evidence that root traits in modern varieties might be more cooperative, their invisibility and difficulty to measure mean that they have been rather understudied in crop breeding. Similarly, the physiological regulation of trait expression and potential interactions between the regulation of different traits have rarely been explicitly considered as breeding targets. An interesting phenomenon in this respect is the apparent interaction that exists between competitive responses to the presence of neighbor plants and expression of defense against pests. Plants respond to light cues reflected from neighbor plants (i.e., light with relatively less red and more far-red) through a set of responses including stem elongation and reduced branching, a syndrome known as *shade avoidance* (Pierik and de Wit 2014). These same light cues have been shown to also suppress expression of defense (Ballare 2014). This has been suggested to reflect a TOC, the idea being that a certain defense expression favors the community as it may deter pests at relatively low costs. A mutant that suppresses

defense may, however, benefit as it foregoes these costs while still benefiting from the pest deterrence provided by its neighbors (Ballare 2014; but see, e.g., Douma et al. 2019). If the expression of this TOC really takes place under farmer field conditions, which still needs to be shown, it would entail a highly interesting breeding target.

Clearly, there are various potential cases for which crop performance could be further improved by selecting for more cooperative traits. The question is to what extent can this be achieved in phenotypic selection methods. This is best achieved through some sort of group selection by growing monocrops of genetic variants and evaluating their performance at the stand level. But it is important to note that in order to maximize the chance of finding the variation that can be used to select for improved plant performance over a range of conditions, one would want to test as many genotypes in as many conditions as possible in the realistic conditions and high densities used by farmers. However, because of limits on space, time, and money, there is a limit to the number of plants one can accurately score in terms of phenotype (Araus and Cairns 2014). The simple solution is to grow only a few individuals per genotype in mixtures. But this enhances the chance of selecting for competitive rather than cooperative traits (Bos 2008), which as noted can be counterproductive to trying to increase population-level performance. This may hold especially for cross-pollinating species, in which maintenance of genetic variation is essential for preventing inbreeding depression, and for evolutionary breeding practices, in which the seed ratio of the next year depends on the yields of the varieties that are grown mixed in genetically diverse stands (Doring et al. 2011). Selection can also directly occur at the individual level through mass selection (Yabe et al. 2013a, 2013b), in which competition between potential targets can be even stronger when these best-performing individuals are grown in higher frequencies at high densities.

Thus, individual selection allows one to test more genotypes under more conditions while group selection allows one to select for less competitive traits. Hybrids of the two could be used whereby, for example, mass selection is applied to the first (few) generation(s) following a cross, and then the most promising varieties are tested in mono-variety groups (kin selection) (Murphy et al. 2017). The balance between the two selection levels (i.e., how much individual versus how much kin) depends on where one expects the greatest yield gains to be achieved: through exploring the overall genetic variation or through directed selection for cooperative traits.

Conclusion and Outlook

An often overlooked characteristic of mutualistic host-symbiont associations is a difference in numbers: in many cases a single host is associated with a group of symbionts. According to this criterion, agriculture is a host-symbiont association in that the farmer generally cultivates fields of crops and herds of livestock. Because of the difference in numbers between partners, domestication is essentially a process of social evolution. Assuming that the symbionts collectively provide a benefit to their host and that resources used for individual competition would divert resources from that collective benefit, an important question is: How can symbionts become and remain social, or behave socially, so that they collectively provide a benefit to the host, and how can the host influence

symbiont sociality, either via genetic selection or phenotypic induction? We considered the two main categories of explanation for social evolution, kin selection and repression of competition, which are not mutually exclusive. Examples of the first category are enforcement of monoculture cultivation by fungus-cultivating insects and selection for social chickens in human agriculture. An example of the second category is the sequestration of “reproductive symbionts” from “worker symbionts,” which has been found in sucking louse gut symbionts. Of note is that in modern human agriculture a similar sequestration of “germline” and “soma” is found, with the germline being provided by specialized seed companies for crops or breeding companies for livestock. An exception to the above-sketches general pattern of increasing sociality of symbionts are mutualisms wherein the benefit of symbionts is based on competitive traits. An example of this category is antibiotic production, which can be selected by interference competition. Another example is a preference for fast-growing crops as found in the mutualism between damselfish and algae (Aanen 2010). In this mutualism, the preferred algae are those that are fast growing and that do not invest in persistent cell walls. In the nonmutualistic situation, these algae are found in the early stages of succession. By their continual weeding, damselfish continuously recreate these early succession conditions. Host interference is a major mechanism to facilitate sociality in a world that is otherwise dominated by individual-level selection and numerous TOCs. This insight can be used more explicitly in agriculture, both in plant and animal breeding, than it is in current practice. There are major unexplored opportunities for selecting at the level of the group in order to improve collective performance of domesticated plants and animals, which usually is correlated with total harvestable yield.

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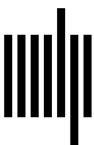
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