of anticodons, counting them as transcribed, before modification of bases, should therefore be 54: one apiece for Phe, Met, Tyr, His, Asn, Asp, Cys, and Trp; two apiece for Gln, Lys, and Glu; three for Ile; four apiece for Val, Pro, Thr, Ala, and Gly; five for Ser; and six apiece for Leu and Arg. Thirty-seven of these have so far been identified in tRNA molecules (*7*). Some of the anticodons in tRNA molecules contain modified first bases (other than hypoxanthine). Such modifications may either restrict (*8*) or extend (*9*) wobble pairing without, of course, engendering ambiguity in amino acid incorporation during peptide synthesis.

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Wolf-Pack Buffer Zones as Prey Reservoirs

Abstract. *In a declining herd, surviving deer inhabited overlapping edges of wolf-pack territories. There, wolves hunted little until desperate, in order to avoid fatal encounters with neighbors. Such encounters reduce wolf numbers and predation pressure and apparently allow surviving deer along territory edges to repopulate the area through dispersal of their prime, less vulnerable offspring into territory cores.*

Predator-prey systems tend to survive for long periods despite the negative effect of the predators. However, the mechanics of the survival process have been little discussed. The process must involve evolutionary strategies of predator, prey, or both, that (i) benefit one or both, (ii) allow the predator to obtain sufficient prey, and (iii) allow enough prey to survive.

One such evolutionary strategy is the tendency of wolves (*Canis lupus*) to prey disproportionately on older animals. Although those predators attempt to catch any prey they can, their physical abilities restrict them to capturing primarily, if not exclusively, disadvantaged or debilitated prey (*1*). Thus wolves can eat, yet their prey populations can themselves survive and produce a crop that wolves can continue to harvest. This strategy requires a precise adjustment of the abilities of both predator and prey.

A second strategy, which relies on the spatial organizations of both predator and prey, is the subject of this report. I recently discovered this strategy in studying drastically declining populations of white-tailed deer (*Odocoileus virginianus*) and wolves in northeastern Minnesota. Deer surviving the decline were distributed almost exclusively along the edges of wolf-pack territories. Although the published evidence is only suggestive (*2, 3*), enough supporting data are accumulating (*4, 5*) to warrant the exposition of a theory of the role of wolf-pack territory edges in the survival of deer populations.

Wolf packs in northeastern Minnesota inhabit a mosaic of adjoining territories of 125 to 310 km^2 each (*6*). Around each territory lies a strip about 2 km wide, the "buffer zone," in which the pack on either side can be found, but in which neither probably spends much time (*7*). Deer usually live throughout wolf territories. Individual deer inhabit areas of 0.48 to 4.10 km^2 in summer and tend during winter to congregate in "yards" as far as 38 km away from summer ranges (*3*).

The precise size and nature of the wolf-pack buffer zone, as well as the behavior of adjacent wolf packs when within it, are unknown. However, evidence indicates that wolves may feel insecure in this peripheral strip and thus may minimize the time they spend there. Wolves will try to kill members of neighboring packs when they meet (*8, 9*), and the maximum chance of an encounter is in the buffer zone. The rate of scent-marking by each pack in the buffer zone is about twice that in the territory center (*7*), which suggests higher anxiety near the territory edge.

One pack of wolves (Harris Lake pack) studied intensively for seven winters killed few deer in its buffer zone when the deer population was adequate to sustain wolf numbers (*2*). However, the deer herd declined rapidly during the next few years as a result of a combination of adverse factors including a high wolf population (*10*). Wolf pups then starved (*9, 11*), wolf productivity dropped (*9*), and wolves became desperate for food (*2*). Only then did packs begin trespassing widely into neighboring territories, and only then did the Harris Lake pack begin killing deer in its buffer zone (*2*). Other packs did likewise.

Meanwhile, the few remaining deer-wintering areas lay in wolf-pack buffer zones (*3, 12*). Deer migrated from them through one or two pack territories and summered in the buffer zones of other packs (*3*). Furthermore, those deer were generally older and had survived longer than deer that had lived throughout the area when the population was higher (*3*). There is little evidence that the deer sought out the buffer zones. Rather, it appears that these animals just happened to live there and that they survived longer because such areas were less used by wolves. Although such interactions became apparent only when the deer to wolf ratio decreased drastically, similar but less extreme interactions probably take place when deer to wolf ratios are more usual.

I propose that these relationships are important in helping to perpetuate the prey population, thereby also helping to perpetuate the predator and, thus, the entire predator-prey system. My theory is that because wolf packs tend to avoid intensive use of buffer zones, deer inhabiting those areas tend to survive longer and form a reservoir for maintaining and recovering deer populations in the wolf territory cores.

This theory implies that when deer populations are high, summer deer densities may be higher in buffer zones than in territory cores, but the disparity will be less than when populations are low, when it may not even be measurable. If deer numbers decline, they will become lowest in wolf-pack territory cores first, and dispersing deer from the buffer zone reservoirs can help replenish the cores. If the decline is too great and wolves are forced increasingly into the buffer zones, the probability of mortal strife (*9*) among wolf packs increases. This tends to discourage pack use of buffer zones and reduces the wolf population (*9*), thus minimizing predation in that area. Because buffer zones would constitute 25 to 40 percent of a region, enough deer would survive there to help repopulate the rest of the area.

Because deer in the buffer zones

would be more secure, they should be older, which is the case (*3*). As their numbers continued to grow in the buffer zones, maturing individuals would eventually disperse and extend their home ranges beyond those in which they were born. With succeeding generations, the home ranges would proliferate and extend farther and farther into the wolf territory cores (*4, 13*). Such deer in their prime have the highest probability of surviving wolf predation (*1*), so they could repopulate the core for several years in relative security. After 4 or 5 years, these colonizing deer might become vulnerable to wolf predation, but by that time, their offspring would be helping repopulate the core along with additional dispersers from the buffer zones. Furthermore, since male deer tend more to disperse and to disperse farther (*4, 13*), chances are better that as the deer herd increased in the territory core, it would contain a preponderance of males. Males are more expendable to a deer herd because deer are highly polygamous.

Winter is the season of greatest vulnerability of adult deer to wolves (*3*), and the proposed theory implies that the more secure (and thus the largest and longest lasting) winter concentration areas would be distributed primarily along wolf-pack buffer zones. This is currently the case in northeastern Minnesota (*3, 12*). The theory predicts and observations confirm that some deer might concentrate in more temporary yards in territory cores, but under adverse conditions those yards are the first to disappear (*10*).

The theory assumes that wolf-pack territory boundaries are relatively stable over long periods. No studies have been conducted long enough in a large enough area to determine whether this is true. However, the Harris Lake pack has occupied the same territory for at least 9 years (*2*) and many of its neighbors have persisted in their territories for several years (*6, 14*). Furthermore the spatial organizations of wolf populations would tend to keep boundaries stable because of the constant territorial "pressure" of all packs (*6*).

I have found only one other proposal that a predator's territorial boundaries serve as reservoirs for prey populations. After publishing the first data on this subject (*2, 3*), I encountered Hickerson's "The Virginia deer and intertribal buffer zones in the upper Mississippi Valley," which presented a strikingly parallel concept. Writing about the buffer zone between the Chippewa and Sioux Indian tribes in Minnesota, Hickerson stated, "Warfare between members of the two tribes had the effect of preventing competing hunters from occupying the best game region intensively enough to deplete the [deer] supply. . . . In the one instance in which a lengthy truce was maintained between certain Chippewa and Sioux, the buffer, in effect a protective zone for the deer, was destroyed, and famine ensued" (*15*). Thus, such a possible evolutionary strategy of a prey species—taking advantage of the spatial organization of predators to provide greater security—should be sought in other predator-prey systems.

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Patterns of Supernumerary Limb Regeneration

In their article "Pattern regulation in epimorphic fields," French *et al.* (*1*) discuss rules which they use to predict the results of a large number of grafting and transplantation experiments in amphibians and insects. Here I show how a well-known mathematical result can be used to derive many of their predictions in a simple and unified way.

In (*1*) it was proposed that each cell has information with respect to its angular position on a growing limb (*2*). This positional information is represented by a digit, 0 through 12, where positions 0 and 12 are identical. Left limbs are represented by a clockwise sequence and right limbs by a counterclockwise sequence. Grafting experiments are represented schematically by giving positional values on two concentric circles, where the outer circle gives positional values on the stump and the inner circle gives positional values on the graft (Fig. 1). The consequences of limb grafting experiments are predicted by use of the following assumptions.

1) When normally nonadjacent positional values are confronted in a graft experiment, growth occurs until cells with all intermediate positional values have been intercalated. The intercalation occurs by the shortest route ("shortest intercalation rule").

2) If, in the resulting map of positional values, a complete circular sequence arises, then a limb will be regenerated whose handedness is predicted by the orientation of positional values around the circle ("complete circle rule for distal transformation").

Figure 1 shows three maps of positional values which were presented in (*1*) to illustrate the application of these rules to grafting experiments. In Fig. 1a no supernumerary limbs are regenerated, in Fig. 1b one right and one left supernumerary limb are regenerated, and in Fig. 1c two right supernumerary limbs are regenerated. The cases shown in Fig. 1, a and b, correspond to grafting a left limb on a left limb stump after rotation by 180°, and the case shown in Fig. 1c corresponds to grafting a right limb on a left limb stump so that anterior-posterior axes are opposed.

The restrictions on the number and the handedness of supernumerary limbs follow immediately from a consideration of continuity properties of a class of maps defined on planar regions. These maps, which I call phase maps, associate to each point in a planar region a phase ϕ,