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.

L. DAVID MECH*
Patuxent Wildlife Research Center,
U.S. Fish and Wildlife Service,
Laurel, Maryland 20818

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* Present address: North Central Forest Experimental Station, St. Paul, Minn. 55108.

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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,

$0 \leq \phi \leq 2\pi$, where the phases 0 and 2π are the same. Except for a finite number of isolated points, called singular points, ϕ is a continuous map from the planar region into the unit circle; ϕ is not defined at the singular points. The diagrams reproduced in Fig. 1 give examples of phase maps in planar regions. For each case the phase maps are constructed in the planar region bound by the large circle which gives positional information on the left limb stump (3 o'clock = $\pi/2$, 6 o'clock = π, 9 o'clock = $3\pi/2$, and so on). Although the singular points are not explicitly shown, the existence of these points is required by the results which follow.

The predictions given by French *et al.* can be interpreted in terms of singular points in phase maps. In the following discussion, ϕ is a phase map defined in a planar region, and C is any closed curve in the planar region which does not pass through a singular point. A remarkable feature of phase maps is that the phases along C place restrictions on the singular points in the area bound by C. These restrictions are made precise in the following way. As C is traversed once in a counterclockwise orientation, ϕ will pass through $2\pi I$, where from continuity I is a positive or negative integer, or zero. The quantity I is called the index of C. For example, in Fig. 1 the index of circles specifying left limbs is -1 and the index of circles specifying right limbs is $+1$. The index of an isolated singular point can be computed by drawing a very small circle A around the singular point so that there is only one singular point in the region bound by A. The index of the singular point is equal to the index of A.

Theorem. The index of C is equal to the sum of the indices of the singular points in the region bound by C (*3, 4*).

I now apply this theorem to the limb grafting experiments (Fig. 1). Here C is the curve specifying positional information on the left stump. The index of C is -1. Hence, the sum of the indices of the singular points in the region bound by C must also equal -1.

Case 1. Left transplant grafted on left stump (Fig. 1, a and b). The index of the curve defining positional information on the left transplant is -1. Consequently the sum of the indices of the singular points in the annulus must be zero $(-1 + 0 = -1)$. If the indices of singular points are restricted to $+1$ (implying right supernumerary limbs) and -1 (implying left supernumerary limbs) then the number of right and left supernumerary limbs generated in the annulus must be equal.

Case 2. Right transplant grafted on left stump (Fig. 1c). The index of the curve defining positional information on the right transplant is $+1$. It is necessary that there exist additional singular points in the annulus. If the indices of singular points are restricted to $+1$ and -1, then there must be two more left limbs than right limbs generated in the annulus $(1 - 2 = -1)$.

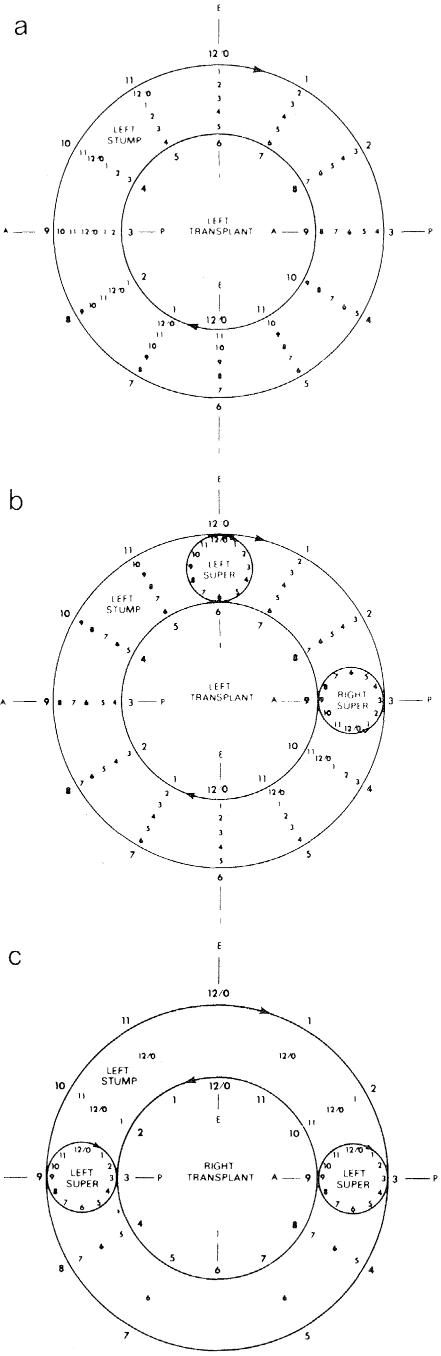

Fig. 1. Schematic representation of positional values in limb grafting experiments, with intercalated positional values, after application of rules described in the text. The outer circle represents the host circumference and the inner circle represents the graft circumference. Clockwise orientations of positional values specify left limbs and counterclockwise orientations specify right limbs. (a and b) Left limb transplanted on left limb stump after rotation by 180°. (c) Right limb transplanted on left limb stump so that anterior-posterior locations are opposed. Abbreviations: *I*, internal; *A*, anterior; *E*, external, and *P*, posterior. [Reproduced from (*1*)]

These restrictions follow from a consideration of the continuity properties of phase maps and do not require a computation of the shortest intercalation route. In one sense, this generalization strengthens the argument in (*1*), since there is no way at present to directly measure the "distance" between different positional values. Note, however, that consideration of continuity alone cannot be used to predict the location of supernumerary limbs or their exact number. Closer analysis of these factors may be helpful in sorting out the details of the intercalation process and may shed light on the underlying cellular and biochemical mechanisms.

The mathematics predict the possibility of other outcomes of grafting experiments in addition to those considered in (*1*). First, there may be singularities whose index is different from $+1$ and -1. For example, a singularity with index $+2$ could generate a double right limb. Also there can clearly be more than two supernumerary limbs.

I emphasize that my goal has been to give a way to predict the consequences of the assumptions in (*1*), but not to critically evaluate those assumptions. There may be ways of specifying positional information other than the polar coordinate system adopted here and in (*1*) that lead to similar predictions about handedness of supernumerary limbs (*5*).

LEON GLASS
Department of Physiology, McGill University, Montreal, Canada H3G 1Y6

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1. V. French, P. J. Bryant, S. V. Bryant, *Science* **193**, 969 (1976). This article should be consulted for references to the experimental literature.
2. Both radial and angular positional values are assigned in (*1*). Here I consider only the angular values.
3. Although this theorem is generally proved for vector fields on planar regions [see, for example, V. I. Arnold, *Ordinary Differential Equations* (MIT Press, Cambridge, Mass., 1973), section 36], it also holds for phase maps as I have defined them. Mathematically inclined readers who wish to pursue the differences between phase maps and vector fields should note that for phase maps defined on oriented, compact surfaces the sum of the indices of the singular points equals zero and that the Euler-Poincaré characteristic of the surface does not enter.
4. Applications of this result in biological and chemical contexts can be found in the elegant studies of A. T. Winfree [*J. Theor. Biol.* **38**, 363 (1973); *Science* **175**, 634 (19 ➡ *ibid.* **181**, 937 (1973)].
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