Data garnered from the number of pelts collected by the fur industry (mostly from the Hudson Bay Co., 1821-1952; and Dominion Bureau of Statistics, 1919-1951) show quite regular cycles of about 10 years for several species in the Canadian boreal forest. Predators include the wolf (Canis lupus), red fox (Alopex lagopus), coyote (Canis latrans), lynx (Lynx canadensis), mink (Mustela vixen), and various hawks and owls. Prey, among others, include the varying hare (Lepus americanus), muskrat (Ondatra zibethica), and ruffed grouse (Bonasa umbellus). The most thoroughly examined data are those pertaining to the lynx and the hare. The former shows a period of 9.7 years, the latter 9.6 years (the difference seems likely to be nothing but statistical noise in the data). Population densities are correlated \((r = .55 \pm 0.5)\), and the lynx population lags, appropriately, behind the number of hares. (Various discussions and treatments of the data can be found in MacLulich, 1937; Elton and Nicholson, 1942; Butler, 1953; and Keith, 1963.) Although it is generally accepted that these fluctuations represent true prey-predator cycles, a number of objections and confounding facts have surfaced. Butler (1953) and Watt (1968) note that fox and lynx populations lag changes in the number of hares by one year since young of the year enter the adult population the next year, this is reasonable. Fisher (1.\(1\) artes pennanti) show a 2-year lag which, in light of this species' habit of delayed implantation, is also reasonable. But coyotes and wolves show even greater lags. Why? Then, on Anticosti Island, Canada, where lynx are absent, an introduced population of hares cycles in phase with its mainland counterparts. Elton and Nicholson (1942) feel that this strongly implicates some endogenous factor. Perhaps the predator population responds to prey numbers, but the prey species cycles as a result of some intrinsic quality-age structure, lags in response to population stress, and so on. But still more seems to be going on. The synchrony of the cycles of mink and muskrat (who do not eat hares) with those of the larger predators (who do) suggests that exogenous events are also important. Moran (1953a and b) feels that the observed cycles are, in fact, driven by prey-predator interactions, but perhaps triggered by exogenous events. Watt (1968, 1969) agrees and presents evidence in support of the idea. For example, statistical analyses of the lynx cycles turns up three clusters of years where the residual (statistically unexplained deviations) errors are huge. One occurs between 2 and 7 years after the eruption of Cosequina, one 3 to 5 years after the eruption of Krakatoa, and one 5 to 6 years after the eruption of Katmai. Watt also finds a highly (statistically) significant correlation between this residual error in lynx numbers and temperature (departure from normal) 3 years previous (the latter is strikingly related to major volcanic events). Finally, there is at least rough synchrony of cycling over most of Canada (but see Section 4.3), suggesting, again, the role of major, external influences. Leslie (1959) had already shown, some time before, that independent (noninteracting) populations, initially cycling out of phase, could be brought into synchrony by random environmental perturbations. More recently, believers of the boreal prey-predator model were
jolted by a paper entitled “Do hares eat lynx?” (Gilpin, 1973). If prey population (n1) is plotted against predator population (n2) as in Figure 4-1, the direction of motion must be counterclockwise, reflecting the lag in predator numbers after those of the prey. But Gilpin found that over some periods of years the direction appeared to be clockwise for the lynx and hares. Perhaps the hares had become, in a sense, the predator by virtue of passing on epidemics to the lynx? He also suggested that the population response by lynx, even where it appropriately lagged its prey, was too quick and too strong. One possible explanation is that the prey-predator cycles are really an interaction between the fur bearers (prey) and the fur trappers (predators). Correlations in lynx and rabbit pelt numbers might arise in the following way. When hares were abundant, trappers might feel free to spend more time trapping the more profitable lynx, but would sit out the rabbit-poor years (Gilpin, 1973). If the cycles were in fact generated in this manner, the rabbit oscillations on lynx-free Anticosti Island would make more sense. Weinstein (1977) takes a somewhat different tack. He finds no evidence of epidemics, and suggests that trappers could ill afford to bypass the poor hare years. But in those poor years, need for food might drive the trappers into areas of low lynx densities. Thus, although a fur bearer-fur trapper cycle is possible, it is also possible that the cycles are not even real, but merely artifacts of the fur records. But Finerty (1979) defends the original premise of MacLulich, and Elton and Nicholson, and feels that the awkward fact of occasional, clockwise plots of prey versus predator are statistical artifacts. Such misleading noise may arise from the fact that cycles are not perfectly synchronized over all of Canada and that the data used by Gilpin were not area-consistent. He cautions that the classical model should not yet be abandoned. The plot thickens with the observation that some Canadian fish populations cycle very nicely in unison with the lynx population (Rowen, 1950). To the north and along parts of Hudson Bay to the east, the boreal forest gives way to tundra, and the 10-year cycle is replaced by a 3- to 4-year cycle (Keith, 1963). Again, the correlation of predator and prey populations, the former lagging the latter, suggest straightforward prey-predator cycles. It is tempting to think that the shift in period is a function of the different species involved, but that would be simplistic; in some cases the species are the same. It is difficult to see how climatic differences, or differences in vegetative dominants, might change the internal dynamics of prey-predator interactions. Why we find a within-biome consistency and an among-biome difference is, at this point, obscure. Let us examine one, closely studied system. In northern Alaska, the brown lemming (Lemmus trimucronatus) undergoes regular 4-year cycles. Lagging by a year are the numbers of owls and jaegers, both lemming predators. Close examination of the dynamics reveals the following details (Pitelka, 1957). Consider a summer of low lemming abundance. High populations of nesting owls and jaegers impose heavy predation, and a sparse grass crop provides little food and little cover. By winter, effects of the low prey density on predator nesting success is apparent, predation declines, and the lemmings escape further decimation. By the following summer
lemming numbers are slightly up, predators have not yet had a chance to reproduce, and the grass is still slightly spared ravages by the still sparse rodents, is recovering. Because lemmings are not yet common, raptor reproduction is mediocre and the next winter finds a continuing increase in both rodents and grass. By the second summer after our starting point, lemmings are abundant and devouring large quantities of grass, and owls and jaegers are having a very successful nesting season. The result is a winter of less grass food, less cover, and heavy predation. The lemmings begin to decline, and continue to do so.