Do changes in female relatedness determine demographic patterns in microtine rodents?

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Lambin and Krebs (1991a) have presented a new model to explain some aspects of population dynamics in voles. Their model is similar to that of Charnov and Finerty (1980) in that it is assumed that voles behave amicably toward kin but aggressively toward nonkin, and that amicable behavior supports population growth whereas aggression opposes it. However, whereas Charnov and Finerty predict that kin associations will be more frequent at *low* density, Lambin and Krebs expect that kin interactions (and amicable behavior) will be prevalent at *high* density, leading to positive feedback on population growth.

In essence, Lambin and Krebs' model argues that differences in winter mortality cause major differences in subsequent population dynamics. They contend that, as populations of voles increase during the breeding season, the average degree of relatedness between neighboring females increases due to philopatry. By the end of the breeding season, the average degree of relatedness, as well as population density, is expected to be high. If winter mortality is high, relatedness among neighbors will be eroded as relatives die and nonrelatives replace them. But if winter mortality is low, levels of relatedness will be preserved. The result is that some populations will enter the next breeding season with low, and others with high, average degrees of relatedness among neighboring females. Lambin and Krebs argue that vole populations starting the breeding season with low relatedness will be subject to severe spring declines caused by aggressiveness, and will not reach high densities that year. In contrast, populations that enter the breeding season with high relatedness will not experience a spring decline and will build to peak numbers that year.

Despite the cautious nature of its title, a query to which the answer must be 'yes', the Lambin and Krebs paper clearly is an attempt to provide a general model to explain patterns of population dynamics in microtines. It is implied that the model is generalizable to microtines as a group, but supporting data come from only a few species. Thus, the paper does not provide an adequate appraisal of the model in light of available data.

The purpose of this note is to point out some assumptions of the model, and expectations arising from it, that are not supported by published data. These assumptions and expectations are as follows: (1) the social system of most voles is characterized by female territoriality in spring with matrilineal kin clusters forming during the remainder of the breeding season; (2) philopatry among females, especially as density increases seasonally, results in higher relatedness at higher population densities; (3) high rates of non-breeding season mortality and immigration are necessary to cause a strong spring decline, which is mediated by female territoriality as breeding commences.

Vole social systems

The generality of Lambin and Krebs' (1991a) model depends in part on the accuracy of their generalization about vole social systems. They claim that vole social systems are characterized by individual territoriality among females in spring, but that "in summer, vole populations contain clusters of related females ..." (p. 127). This change occurs because in summer, "food resources are becoming more abundant than in early spring and females can breed in non-exclusive home

ranges or have smaller territories." (p. 127). Later, they weaken the generalization by stating, "Thus in some species females are territorial during the whole breeding season while in other species female territoriality is restricted to the beginning of the breeding season (Lambin and Krebs in press.)" (p. 128). This latter statement is a more accurate reflection of vole social organization than is the former, but is not consistent with a general model based on a common social organization in arvicolids.

A wealth of evidence indicates that in many species of vole, females maintain exclusive territories, and are *overdispersed* through most of the breeding season (Bujalska 1990, Madison 1990, Ostfeld 1990). This is in marked contrast to *Microtus californicus, M. townsendii, M. xanthognathus* and *M. agrestis*, in which females overlap extensively in a clumped or random distribution through most of the breeding season (Myllymäki 1977, Wolff and Lidicker 1980, Ostfeld 1986, Heske 1987, Lambin and Krebs 1991b). Thus Lambin and Krebs' model may pertain only to a minority of vole species in which females aggregate.

In one of the best-studied vole species, *M. pennsylvanicus*, females associate in dyads in spring, and become more solitary and territorial in summer (Madison and McShea 1987). Lambin and Krebs point out several other instances in which some females in a vole population share space in spring, but not in summer. This pattern is opposite that assumed by Lambin and Krebs to be general.

Female philopatry and relatedness of neighboring females

A critical component of Lambin and Krebs' model is that female voles are philopatric. Philopatry would cause an increase in average degree of genetic relatedness among neighboring females as density increases over a breeding season. This assumption would be undermined by data demonstrating that dispersal of females is common, that it increases over the course of a breeding season, or that it increases with population density.

Lambin and Krebs predict that the average degree of relatedness among neighboring females increases over the course of a breeding season and with increasing density. High relatedness is assumed to be the proximate cause of a lack of aggression and high reproductive rates at that time. In contrast to this prediction, numerous studies indicate that in many vole species, the number of dispersers increases with population density (Gaines and McClenaghan 1980). Unfortunately, most of these studies were not designed to detect successful immigration, which is more important than emigration in affecting genetic relatedness within groups. However, a *decreasing* degree of genetic relatedness among

neighboring voles (i.e. decreasing F_{ST}) with increasing density has been documented in *M. californicus* (Bowen 1982). F_{ST} measures genetic heterogeneity among groups, or demes, and it is not specific to female neighbors (Kawata 1990). Therefore, it is possible that the decreasing F_{ST} reflected behavior of males and nonreproductive individuals, swamping an opposite pattern in females. However, this seems unlikely owing to the strongly female-biased adult sex ratio in high-density populations of *M. californicus* (Cockburn and Lidicker 1983, Ostfeld et al. 1985, Ostfeld and Klosterman 1986, Heske 1987).

Pugh and Tamarin's (1990) study of *M. pennsylvanicus* showed that there was very little spatial association between adult relatives of either sex. On one trapping grid the average coefficient of relationship (Hamilton 1964) among neighboring adult females decreased with increasing density, and on another it increased slightly. However, the average coefficient of relationship among neighboring females was always < 0.25, and usually < 0.10 (Pugh and Tamarin 1990). These results do not support Lambin and Krebs' model.

Finally, Lambin and Krebs seriously confound relatedness and familiarity as potential causes of reduced aggression in voles. Despite their discussion of this topic (Lambin and Krebs 1991a: 129–130), they fail to recognize the degree to which their model is debilitated if familiarity is the proximate basis for relaxed aggression. If level of aggression among females is determined by familiarity, then spring aggression should be directed only at recent immigrants. There also should be little or no aggression between adjacent females that are established, although unrelated, neighbors during the breeding season. Clearly, if low aggression coincides with high familiarity, the genetic relatedness of neighboring females becomes much less relevant than proposed by Lambin and Krebs.

Winter mortality, immigration, and spring declines

A critical component of Lambin and Krebs' model is that severe spring declines are expected to follow winters in which mortality and immigration erode the high genetic relatedness among members of overwintering groups. Little or no spring decline will occur in years during which high relatedness is preserved by good overwinter survival. Two assumptions underlying this scenario are: (1) overwintering groups typically are composed of related females; and (2) mortality is necessary to change overwintering group composition. A prediction arising directly from this scenario is that spring declines will be disproportionately more severe in low-spring-density populations (in which relatedness is low) than in high-spring-density populations. Are the assumptions and prediction supported?

Although overwintering aggregations are common among arvicolids (e.g. Wolff and Lidicker 1980, Madison 1984), the genetic relatedness among group members is known for few species. Data from wintering *M. pennsylvanicus* are in apparent support of Lambin and Krebs' assumptions; nesting groups are sometimes composed of relatives, predation reduces group size, and transfer of individuals among groups is coincident with the reduction of group sizes (Madison et al. 1984). However, nesting groups are characterized by male-male and male-female associations; female-female associations occur at a significantly lower frequency than that expected by chance pairings (Madison et al. 1984). Thus, the expectation that overwintering groups are matrilineal does not appear to be met in this species.

In *M. xanthognathus,* summer associations among relatives are disrupted by dispersal just before and during the formation of wintering groups. This behavior leads to nesting groups the members of which are unrelated (Wolff and Lidicker 1981). Although *M. xanthognathus* does not appear to undergo cycles (Wolff and Lidicker 1980), their annual peak densities are of a magnitude similar to multiannual peaks in cyclic species from comparable habitats (Hansson and Henttonen 1985). In this species at least, a lack of kin association during winter does not lead to a heavy spring decline and low density, a result that opposes the Lambin and Krebs model.

Two experimental studies of the effects of winter density on the magnitude of spring declines are in direct opposition to the prediction that spring declines should be more severe when overwinter density is low (Lambin and Krebs 1991a). Boonstra (1977) found that an experimental reduction of density in autumn and winter, as well as just before spring breeding, *improved* survival of female *M. townsendii* in spring. Rodd and Boonstra (1984) performed a similar density-reduction experiment on *M. pennsylvanicus,* and found that autumn and spring removals increased or did not change survival of females later that spring, and that breeding began earlier on removal grids.

Finally, it is important to note that males tend to be more severely affected by spring declines than are females in many species of voles (e.g., Krebs and Boonstra 1978, Rodd and Boonstra 1984). This observation undermines the assumption of Lambin and Krebs that the magnitude of spring declines is a direct consequence of agonistic behavior among females. It is well documented that territoriality and spacing behavior operate within, but typically not between, sexes (Boonstra and Rodd 1983, Ostfeld 1985). Thus, the causes of spring declines are not as simple as described by Lambin and Krebs.

Conclusion

Lambin and Krebs (1991a) have provided a mechanism to explain the common pattern in voles and lemmings that a peak year follows a winter in which breeding occurs and survival is good. However, their mechanism invokes a common social organization among voles, a seasonal increase in the relatedness of neighboring females over summer owing to philopatry, a seasonal decrease in relatedness over winter mediated by predation and immigration, nepotism by females, and the regulation of spring declines by the average relatedness among neighboring females. None of these assumptions and predictions can be generalized to microtine rodents as a group, some may be true for some species, and others need further testing. Moreover, it seems more logical to expect that good overwinter survival and winter breeding will *by itself* cause early and rapid population growth often leading to peak density.

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