Is the indirect predator effect a special case of generalized reactions to density-related disturbances in cyclic rodent populations?

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The indirect predator effect is put into the wider context of a 'general sensitivity syndrome', including e.g. variable sexual maturation, low sociability, high activity levels and larger body size in voles from cyclic populations. Such animals respond by lowered reproduction to the presence of conspecifics, related species and predators. Differences with regard to animals from noncyclic populations appear to be genetically based. The pure presence of predators may or may not, depending on intraspecific reactions, affect final densities of local vole populations negatively but regional growth rates will possibly be affected positively.

1. Introduction

Effects of pure predator presence on small rodent reproduction (especially of the bank vole *Clethrionomys glareolus*) has attracted considerable interest during recent years (Ylönen 1989, Heikkilä et al. 1993, Korpimäki et al. 1994, Ylönen & Ronkainen 1994). Several laboratory experiments have shown voles to react by delayed maturity or reduced reproduction to the presence of mustelids, and field observations, including field experiments (Korpimäki et al. 1994), have provided crucial support.

Other experimental studies have demonstrated a greater sensitivity in the reproduction of voles (*C. glareolus*) from cyclic than from non-cyclic areas to other disturbance than predator presence (Hansson 1990). Furthermore, individuals from cyclic vole populations deviate also in other characteristics from their noncyclic conspecifics, i. e. under experimental conditions being sensitive to intraspecific disturbance in sexual maturation (Gustafsson et al. 1983a), in being less sociable and more aggressive (Hansson 1986), more active (Rasmusson et al. 1977, Nygren 1978, Ebenhard 1987), larger (Gustafsson et al. 1983b, Hansson 1993) and in having female-biased sex ratio at birth (Hansson 1987). Field data also demonstrate more irregular reproduction in cyclic populations (Hansson & Henttonen 1985a, Stenseth et al. 1985). A more general syndrome of greater sensitivity to social and environmental conditions thus occurs in cyclic animals and the reaction to predator presence may be put into this wider context. Below, I reexamine older data (Hansson 1990) and provide new ones to be able to compare intraspecific reac-

tions in cyclic and noncyclic *C. glareolus* females with indirect predator effects.

2. Material and methods

Bank voles were caught in autumn 1980–92 in four Swedish localities at an age of 1–2 months and were brought alive to a laboratory at Uppsala for breeding. Only the southernmost population, at Revinge, was consistently noncyclic (Hansson & Henttonen 1985b, Hansson 1994). Animals from the other populations were pooled as cyclic for 1980–1988. However, no cyclic dynamics could be detected in the northern populations in 1990–92 (Hansson 1994) and they were then termed 'previously cyclic'. The animals were kept in laboratory mouse cages with 25–50 cages in close proximity in each room. They were bred as monogameous pairs at constant temperature and food (ad lib.) and at ambient light for one year, i.e. to the normal maximum age. The proportion of females producing at least one litter and the number of litters produced was established for each pair. Young born in late summer-autumn (lab-born generation) were paired randomly and bred in the same way for another year.

3. Results

Significantly fewer cyclic and field-born bank voles produced any young in 1980–88 than the noncyclic animals from the same period (Table 1; $\chi^2 = 11.67$, $P < 0.001$). Field-born animals from

Table 1. Frequencies of female *Clethrionomys glareolus* reproducing in the laboratory, based on animals collected in different population types.

Population type	Years	Field-born generation		Lab-born generation	
		n	%	*n*	%
Cyclic	1980–88	105	28	35	54
	Peak years	26	27		
	Other years	79	28		
Noncyclic	1980–88	63	54	36	42
Previously cyclic	1990–92	53	15	39	33
Consistently noncyclic	1990–92	36	39	102	54

previously cyclic areas still reproduced less well in captivity in 1990–92 than consistently noncyclic animals ($\chi^2 = 6.52$, $P = 0.01$). Laboratory-born females from previously cyclic areas differed in reproduction from offspring of consistently noncyclic females in 1990–92 ($\chi^2 = 4.79$, $P < 0.05$) but not in 1980–88 ($\chi^2 = 1.13$, *NS*). The number of litters was also greater for females caught in noncyclic than in cyclic populations in 1980–88 (Table 2: $t = 2.55$, $P = 0.01$). There was no corresponding difference in the litter numbers of the mature offspring of the two types of animals ($t = 0.24$, *NS*) but confidence limits were very wide for the second generation from cyclic areas.

4. Disscussion

It is clear that reproductive failure, especially in animals of cyclic origin, was partly a laboratory artifact. It might have been due to confinement in small cages or the smell of, or other disturbance from, conspecifics. Long-term monogameous pairing is also a possible reason. However, the difference between the two population types makes it an important indicator of natural differences in sensitivity. If monogameous pairing is a main reason, then change of mating or breeding sites should be more common in cyclic animals. As Gustafsson et al. (1983a) got different sexual development of *C. glareolus* with different proximity of conspecifics, the olfactory (and possibly acoustic or tactile) environment may have been more important for reproductive inhibition than confinement per se.

It seems likely that the greater sensitivity to 'general disturbance' in cyclic animals has developed as a generalized adaptation to the great densities at population peaks. Sensitivity to high

Table 2. Litter numbers of *Clethrionomys glareolus* in the laboratory, based on animals collected in different population types.

Population type	Years	Field-born generation			Lab-born generation		
		n	*x*	*SD*	*n*	*x*	*SD*
Cyclic	1980–88	18	4.4	2.0	19	5.3	4.1
Noncyclic	1980–88	34	5.7	2.0	15	5.6	3.2

density conditions in cyclic populations in order to counteract fitness sinks might include aversive reactions to, and withdrawal from, the proximity of conspecifics and related species (see Viitala 1984) in order to avoid severe competition for food, aversion to animals of the same sex in order to avoid competition for mates, aversion to changes in the close environment in order to avoid areas with degraded habitat, and aversion to the close presence of predators in order to avoid being eaten. Ebenhard (1987) suggested a higher level of emigration in northern cyclic voles. The behavioural and physiological responses observed would tend to cause diminished population growth in centres of high density, but increased population growth in a larger area or region.

This adaptation appears to have a genetic background. The sensitivity in both breeding frequencies and in number of litters changed to some extent between field animals and the laboratory-born animals produced by the field animals. The high variability in numbers of litters in laboratory-born offspring of previously cyclic animals may be one indication that selection was going on. Furthermore, a fairly large number of noncyclic animals also refrained from breeding under laboratory conditions. There was evidently variability for selection to work on in originally noncyclic areas. On the other hand, the change was very gradual as there was no difference in the reactions of animals from peak and low years and no difference between populations that changed from cyclic to noncyclic dynamics (Table 1). Thus, there was still not the rapid selection for aggressive behaviour that is assumed in the Chitty hypothesis of population regulation (Krebs 1978).

The suggested 'general sensitivity syndrome' would predict a weaker reaction, or absence of reaction, of noncyclic voles to the presence of mustelids. This prediction was at least partly supported by the laboratory findings by Heikkilä et al. (1993). It also predicts that heavy removal of voles by mustelids may dampen the intraspecific sensitivity reactions by surviving animals. The proximate influence of the pure presence of mustelids on vole reproduction may not affect final densities if there is still some reproduction and population growth: To demonstrate a numerical effect it should be shown that the indirect predator effect is additive

to effects of intraspecific sensivity reactions at high density. The indirect predator effect may well increase population growth regionally by induced dispersal.

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