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Parent-offspring correlations for growth and reproduction in the vole *Clethrionomus glareolus* in relation to the Chitty Hypothesis

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Abstract

Studied in laboratory correlations between parents and offspring for weights and reproductive parameters in voles *Clethrionomys glareolus* from a non-cyclic population. Weight correlations were significantly positive in males and negative in females. Reproductive parameters correlated negatively. The latter correlations could be analysed further and be interpreted as due to a negative maternal effect. These findings contradict the Chitty Hypothesis of population regulation but may explain cyclic variations in weight and reproduction if external factors drive the cycles.

Introduction

Microtine cycles are characterized by small animals with high reproductive output during the increasing phase and large, slowly-reproducing animals at peaks. However, small adult animals with low reproduction occur during the declining phase (Krebs and Myers 1974; Taitt and Krebs 1985).

The Chitty Hypothesis (Chitty 1967, 1970, cf. also Krebs 1978), predicting regular genetic changes with cyclic fluctuations, has had a profound impact in explaining such morphological and reproductive variations. It states that timid, slowly-growing but high-reproducing animals are favoured in sparse and increasing pupulations whereas aggressive, large but slowly-reproducing animals are favoured in dense or peak populations. This mashinery should drive the cycles. Body growth and reproductive rates should thus be mainly genetically determined in microtine populations; body size and reproductive output should be closely correlated between parents and offspring. Animals caught in various population phases and brought to a laboratory should retain such correlations if there is low or random (density-independent) selection in the laboratory. These predictions were examined on the bank vole *Clethrionomys glareolus* which appears in both cyclic and non-cyclic populations in Sweden (Hansson and Henttonen 1985a).

Methods

The study was performed on animals which were bred for other reasons (Hansson and Henttonen 1985b; Hansson 1986) under laboratory conditions. The founding animals were taken from a clearly non-cyclic population in south Sweden (Hansson and Henttonen 1985a). Thus, it was possible to evaluate parent-offspring relations with regard to the pattern of population dynamics. The data were examined according to the rules of quantitative genetics but the relationships were mainly expressed as correlations (cf. Millar 1983) since certain prerequisites for heritability analysis may not have been present.

Bank voles were caught in live traps at Revinge (56° N) in 1980–83. The animals were kept as monogamous pairs after capture so the low mortality (19 and 8 % per year for wild-caught and

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laboratory-born animals respectively) was not density-dependent. The voles were caught in early autumn as young animals and kept on constant food (laboratory mouse pellets) and at a constant temperature (20 °C) for one year or until reproduction ended. Young of these animals, born in late summer-early autumn, were kept as monogamous pairs from an age of four months under the same laboratory conditions. Males were weighed every second week and the maximum weights recorded for each individual was used for the computations. In females, pregnancies caused exceptional weights so instead the weight one month before the first parturition was used. The length of pregnancy is ca 20 days in this species. Times of first parturition, litter sizes and number of litters as well as the total number of weaned young were recorded for all field-caught females (P) and their female offspring (F_1). Correlations were examined between weights and reproductive parameters of field-caught animals and the corresponding means of their laboratory-born offspring (Falconer 1981).

Results and discussion

Males showed a strong positive correlation in weights between parents and offspring (Table 1). Females showed a negative correlation, on the border of significance, for the same relationship. The number of litters, number of weaned young, mean litter size and start of reproduction were all consistently but non-significantly negatively related between female parents and offspring (Table 2).

Table 1. **Correlations between maximum body weight (see text for estimation) of P and F_1 *Clethrionomys glareolus***

Sex	N	r	P
Males	12	0.81	< 0.01
Females	12	− 0.52	~ 0.05

There were thus clearly positive parent-offspring relationships in the body weights of the males. The mean weight ($\bar{x} \pm SD$) of parent (P) males was 24.3 ± 2.4 g and of offspring (F_1) males 23.8 ± 3.0 g so there was no significant change due to laboratory breeding. These relations have to be interpreted as genetic as no sources of error would cause a change in that direction for males (cf. below for females). The regression coefficients ($b \pm SE$) were 1.02 ± 0.24. According to Falconer (1981), this indicates a very high level of heritability. The generally negative relations in both body weights and reproductive parameters between female parents and offspring have to be interpreted as "a negative maternal effect" in analogy with Leamy (1981) and Millar (1983). Both these authors got consistent but low and often non-significant negative correlations in these parameters for both *Peromyscus leucopus* and *P. maniculatus*. They suggested that these negative correlations were due to well-fed females giving birth to large litters, where however each young had a low body weight. The female young were supposed to retain a comparatively low body weight as adults, to reproduce late and to produce small litters.

Table 2. **Correlations between reproductive parameters (see text for estimation) of P and F_1 *Clethrionomys glareolus***

Reproductive parameter	N	r	p
Number of litters	13	− 0.25	NS
Weaned young	13	− 0.23	NS
Litter size	8	− 0.34	NS
Start of reproduction	8	− 0.40	NS

The applicability of this interpretation was examined as regards litter sizes and weight at weaning (Table 3). Litter sizes were significantly larger in the wild-caught (P) than in the laboratory-bred (F_1) females while female young at weaning (20 days) were heavier, although not significantly so, in the litters of F_1 females. However, a significantly lower

Table 3. **Litter size and female weaning weight in litters produced by P and F_1 *Clethrionomys glareolus* females, weighed before breeding started**

	Weight before breeding				Litter size				Weights of female young at weaning			
Mothers	N	$\bar{x}$	SD	Significance	N	$\bar{x}$	SD	Significance	N	$\bar{x}$	SD	Significance
P	40	18.5	2.1	P<0.001	141	4.9	1.2	P<0.05	219	9.1	1.9	NS
F_1	35	16.0	1.9		85	4.5	1.4		77	10.0	1.5	

weight had appeared at maturity in the F_1 females from P litters. Thus a negative effect due to alternating large and small litters was supported also by the present data. It is obviously due to limited body resources (energy or nutrients) and the mobilizable amounts of these resources are probably related to body size.

The correlations in Table 2 are not significant. However, the interpretation of them as maternal effects on reproduction is supported both by similar findings in two American small rodent species and by significant differences in a derived relationship between litter sizes and female weights. Thus, although the reproductive effects are not as evident as the correlations in body weight both may be used for evaluating ideas relating to weight and reproduction in free-living populations.

One of the correlates of the proposed mechanisms in the Chitty Hypothesis for cyclic vole populations, i.e. a strong heritability of male body weights, was thus observed also in a non-cyclic vole population, thereby indicating a lack of importance of this factor in population dynamics. The negative maternal effect may be important in the demography of cyclic populations if the cyclicity is caused by other factors. In the present study it was observed under the same nutritional conditions for parents and offspring. However, the body growth improved in animals taken into the laboratory from the field and given surplus food (Hansson 1985, unpubl.). In an increasing vole population there is more food per individual than in a peak population. Thus, the negative maternal effect should be much more obvious under field conditions in peak/decline populations. It may at least partly explain why increase-early peak animals reproduce early and have larger litters (Hansson and Henttonen 1985b) and why late peak-decline animals show low body weight and late start of breeding, as evident for *C. glareolus* in, e.g., Hansson (1984).

Summarizing, selective effects on individual characteristics related to body size do not cause vole cyclicity according to the Chitty Hypothesis while reproductive patterns in vole cycles, also appearing in the Chitty Hypothesis, may be explained by alternating positive and negative maternal effects.

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Zusammenfassung

Korrelationen von Wachstum und Reproduktion zwischen Eltern und Jungtieren bei der Rötelmaus Clethrionomys glareolus in Beziehung zur Chitty Hypothese

An nicht zyklischen Populationenen von *Clethrionomys glareolus* wurden Korrelationen von Wachstum und Reproduktion zwischen Eltern und Jungtieren untersucht. Die Wechselbeziehungen in der Körpergröße waren positiv bei männlichen und negativ bei weiblichen Individuen. Die Wechselbeziehungen in bestimmten Fortpflanzungsparametern waren negativ und wurden weiter analysiert. Sie könnten durch einen negativen maternalen Effekt bedingt sein. Diese Befunde widersprechen der Chitty Hypothese zur Populationsregulierung, könnten aber die zyklischen Variationen von Gewicht und Reproduktion erklären, wenn äußere Faktoren die Zyklen beeinflussen.

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