

S38-5 Are unseen effects of early environment negligible? Three examples in great tits (*Parus major*)

Arie J. VAN NOORDWIJK

Netherlands Institute of Ecology, P.O. Box 40, NL 6666 ZG Heteren, The Netherlands; noordwijk@cto.nioo.knaw.nl

Abstract Three case studies failed to demonstrate impacts of early environment or maternal effects on breeding in situations where they could have been expected. This leads to a number of methodological questions about the resolving power required to detect such impacts, but above all else to the conclusion that maternal effects and homeotic control are opposites. When assessing potential maternal effects, one has to consider not only the developmental period in which they occur but also the later stage of life of concern, because, with age, maternal effects may become less and less important or disappear altogether. The only real measure that there is of the relative importance of early environment and maternal effects is their proportion in phenotypic variance in the traits of interest.

Key words Environmental effects, Maternal effects, Breeding, Great tit

1 Introduction

There is abundant evidence from invertebrates that environmental conditions during early development have effects that last throughout life (Prout, 1984, and references therein). Yet homeostatic regulation and compensatory growth processes may lead to the disappearance of early effects, particularly in homeotherms with finite growth. Thus, in searching for lasting effects from early environment, we have to consider not only the traits of concern and environmental factors during the period of development under investigation, but also those later stages of life that may express the effects. For morphological traits including body size, regulation of growth determines the time window for environmental effects on the phenotype, because, in animals with determinate growth, there can be no compensatory growth after growth has stopped (van Noordwijk et al., 1988; Alatalo et al., 1990; Larsson, 1996).

Demonstrating that effects are absent requires the capacity to demonstrate their presence with sufficient power to find the smallest effects of concern. This is more difficult than demonstrating simple presence, for a number of reasons: first, the adequacy of the methods required is more critical, secondly, the specificity of the effects sought is more critical, and thirdly, it is more difficult to find a good frame of reference for the negligibility of the effects. I present here three examples where three different aspects of the early environment could have, but did not, explain a significant part of phenotypic variation (Table 1).

2 Example 1: laying date of females hatched in a second brood

A number of studies have shown a heritable compo-

nent in the timing of reproduction in the great tit, *Parus major* (van Noordwijk, 1981; van der Jeugd and McCleery, 2002); but in contrast to factors such as clutch size, the environmental component is complex and heritability estimates are sensitive to outliers (van Noordwijk, 1981). Opportunities to test the effect of early environment on subsequent timing of reproduction are provided by females that produce a second clutch. Second clutches are always produced by early laying females (Verboven and Verhulst, 1996). Thus, great tits recruited from a second clutch should be genetically early, but very late in terms of juvenile environment. In mainland European populations, the number of local recruits from second clutches is very low. This may be a consequence of lower post-fledging survival or a higher tendency to disperse or both (Dhondt and Huble, 1968). However, in the island population on Vlieland, the number of local recruits from second broods is quite high (van Balen et al., 1987). In the period between 1956 and 1995, 91 females hatched in second broods were recruited into the breeding population.

In order to evaluate the reasons for this, I compared the laying dates of females hatched from a second clutch with those hatched in a first brood (Table 1). The females hatched in second broods were found to be early breeders. Their advancement was related to the extent to which females producing a second clutch are early relative to the total population (van Noordwijk, in prep.). We can characterize the difference in first clutch laying dates between females producing a second clutch and the total population as a selection differential, and the deviation of laying dates in second brood-hatched females from the total population as a response. This allows calculation of realized heritability for the group.

Table 1 Summary of examples from studies of the great tit (*Parus major*)

Trait	Environmental effect	Age of effect	Age of testing for effect	Type of test
Laying date	rearing environment in early May versus late June	whole nestling period	first year breeders	difference in laying date between individuals hatched in 1st or 2nd brood
Fledging weight	quality of pair or territory related to clutch size	nestling period	prior to fledging	comparison of fledging weights, balanced for date between broods differing in original clutch size
Behavior score	feeding behavior of foster pairs	1–10 days after hatching	40 days after hatching	behavior scores of birds from up and down selection lines raised together

The values obtained for realized heritability varied from 0.55 to 0.22, depending on whether outliers were included or ignored. The values, however, are the same as for heritability based on daughter-mother similarities in recruits from first clutches. The conclusion that there are no detectable effects from being hatched six weeks late is thus quite strong, as second-hatched females could have been expected to lay many days late, but not one day early. There may thus be a buffer period in the annual cycle that is long enough to absorb the effects of hatching six weeks late.

3 Example 2: fledging weights in relation to parental clutch size

In the context of a selection experiment on clutch size in a natural population of great tits, large numbers of clutches were raised by pairs which had produced either bigger or smaller clutches (van Noordwijk et al., in prep). In this reciprocal selection experiment, about 35 broods were cross-fostered each year and then matched for laying date with broods raised by the biological parents. There was a systematic difference of two eggs in the clutch sizes of donor and foster parents. Had clutch size been indicative of the quality of the pair and or their territory, substantial differences in fledging weights could have been expected. In none of five years, nor in either of the two directions (lighter or heavier nestlings), was there any significant difference (Table 1). In fact, in five out of the ten cases, what small difference there was was in the direction of parents of larger clutches producing lighter rather than heavier fledglings when raising broods of the same size, contrary to expectations. In two cases no difference was found, and only in three was the difference in the expected direction. Although potentially detectable difference in each individual replicate was limited because of the standard error of the average of brood means (0.2–0.4 g), the combined power of the ten replicate tests would have allowed detection of average differences in the order of 0.15 gram or about one per cent of average fledging weight.

4 Example 3: rearing environment scored on behavior

Great tits were selected for exploration behavior, measured around 40 days after hatching (Drent et al., 2002).

Chicks raised in broods in the field were mixed between up and down selection lines, so that all chicks grew up in an environment with sibs of both types (Table 1). The chicks were then taken to the laboratory at ten days after hatching for hand-raising, where they remained in mixed groups. Thus, if their early environment, and in particular their feeding during completion of brain growth, had had a strong effect on later behavior, one would have expected an effect from foster brooding in their behavior score. Although such an effect has been found in mice (Benus and Henkelman, 1998), no effects of a fostering environment were found in this case.

5 Conclusions

In each of these examples, we may conclude that aspects of early environment did not explain a biologically and statistically significant part of phenotypic variation at specified later stages in life. There may well be other aspects of the environment that do have a lasting effect, even for the same traits. These effects will have to be investigated one by one. It is therefore crucial to tease out the potentially important impacts of early environment into a number of testable components (van Noordwijk, 1989). In order to do this, guidelines are needed for determining which effects to test on what traits. It seems to me that the only reasonable guideline is provided by observed phenotypic variance in traits under natural environmental conditions. In explanations of such variance, the proportions that can be attributed to maternal or early environmental effects then serve as a measure of the importance of those effects.

References

- Alatalo RV, Gustafsson L, Lundberg A, 1990. Phenotypic selection on heritable size traits — environmental variance and genetic response. *Amer. Nat.* 135: 464–471.
- van Balen JH, van Noordwijk AJ, Visser J, 1987. Lifetime reproductive success and recruitment in two great tit populations. *Ardea* 75: 1–11.
- Benus RF, Henkelmann C, 1998. Litter composition influences the development of aggression and behavioural strategy in male *Mus domesticus*. *Behaviour* 135: 1 229–1 249.
- Dhondt AA, Huble J, 1968. Fledging date and sex in relation to dispersal in young great tits. *Bird study* 15: 127–134.
- Drent PJ, van Oers K, van Noordwijk AJ, 2003. Realised heritability of personalities in the great tit (*Parus major*). *Proc. R. Soc. Lond. B* 270: 45–51.
- van der Jeugd HP, McCleery R, 2002. Effects of spatial

- autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *J. Evol. Biol.* 15: 380–387.
- Larsson K, 1996. Genetic and environmental effects on the timing of wing moult in the barnacle goose. *Heredity* 76: 100–107.
- van Noordwijk AJ, 1989. Reaction norms in genetic ecology — studies of the great tit exemplify the combination of ecophysiology and quantitative genetics. *Bioscience* 39: 453–458.
- van Noordwijk AJ, van Balen JH, Scharloo W, 1981. Genetic variation in the timing of reproduction in the great tit. *Oecologia* 49: 158–166.
- van Noordwijk AJ, van Balen JH, Scharloo W, 1988. Heritability of body size in a natural population of the great tit (*Parus major*) and its relation to age and environmental conditions during growth. *Genetical Research* 51: 149–162.
- Prout T, 1984. The delayed effect on adult fertility of immature crowding: population dynamics. In: Wbhrman K, Loeschcke V ed. *Population Biology and Evolution*. Heidelberg: Springer Verlag, 83–86.
- Verboven N, Verhulst S, 1996. Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. *J. Anim. Ecol.* 65: 264–273.