MATERNAL INHERITANCE OF CONDITION AND CLUTCH SIZE IN THE COLLARED FLYCATCHER

DOLPH SCHLUTER
Ecology Group, Department of Zoology, University of British Columbia,
Vancouver, BC V6T 1Z4, CANADA

AND

LARS GUSTAFSSON
Department of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, SWEDEN

Abstract.—Maternal effects may strongly influence evolutionary response to natural selection but they have been little studied in the wild. We use a novel combination of experimental and statistical methods to estimate maternal effects on condition and clutch size in the collared flycatcher, where we define "condition" to be the nongenetic component of clutch size. We found evidence of two maternal effects. The first (m) was the negative effect of mother's clutch size on daughter's condition, when mother's condition was held constant. The second (M) was the positive effect of mother's condition on daughter's condition, when mother clutch size was held constant. These two effects oppose one another because mothers in good condition also lay many eggs. The maternal effects were large: Experimentally adding an egg to a mother's nest reduced clutch sizes of her daughters by ¼ egg (i.e., $m = -0.25$). Measured degree of resemblance between mother and daughter clutch sizes yielded $M = 0.43$. The results weakly support the presence of heritable genetic variation in clutch size: additive genetic variance/total phenotypic variance = 0.33. This estimate was highly variable probably because, as we show, mother–daughter resemblance may depend hardly at all on the amount of genetic variance when maternal effects are present. Daughter–mother regression (a standard method for estimating heritability) is consequently a poor guide to the amount of genetic variance in clutch size. Our results emphasize the value of combining field experiments with observations for studying inheritance.

Key words.—Clutch size, condition, heritability, life-history evolution, maternal effects.

The rate and direction of evolution depends on the mechanisms by which parents pass their traits to offspring. Most efforts to measure resemblance of offspring to parents have focussed on the genetic basis, as summarized by the heritability (Falconer, 1981). However, maternal effects may strongly influence evolutionary response to natural selection (Kirkpatrick and Lande, 1989; Cowley and Atchley, 1992; and references therein), but they have been much less studied in wild populations than genetic effects (Falconer, 1981; Price and Grant, 1985; Roach and Wulff, 1987; Janssen et al., 1988; Lande and Price, 1989; Mousseau and Dingle, 1991). The maternal basis of variation in most traits is unknown.

In this paper we estimate genetic and maternal influences on clutch size in a population of collared flycatchers (*Ficedula albicollis*). Clutch size is an interesting trait for a study of inheritance for several rea-

sons. It is a life-history trait closely linked to fitness. It is also expected to have a large nongenetic component associated with nutrition, because clutch size in birds can often be increased by providing supplemental food to parents (Drent and Daan, 1980; Daan et al., 1990; L. Rowe, D. Ludwig, and D. Schluter, unpubl. MS). Conceivably, a mother in good physical condition could raise daughters of higher than average condition, who in turn would lay a larger number of eggs. Alternatively, the large clutch produced by a mother in good condition could dilute her parental care among more young, with negative effects on the condition and subsequent clutch size of each daughter (Lack, 1966). We investigate how these potentially opposing maternal influences are resolved.

Clutch size is known to be "heritable," in that mothers laying many eggs tend to produce daughters that lay many eggs. For ex-
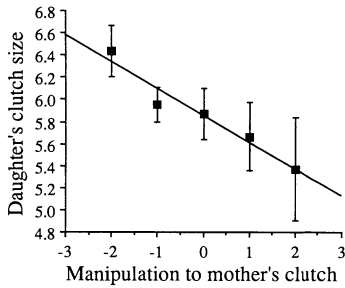
FIG. 1. The relationship between experimental change in hatchling number (corresponding to a change in clutch size) to a mother's nest, and the ensuing clutch size of daughters in their first year of breeding.
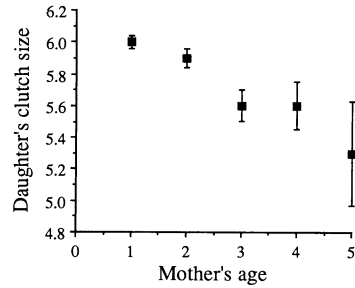

FIG. 2. Relationship between mother's age (in years) and clutch size of daughters in the daughter's first year of breeding. Vertical bars denote standard errors. Slope $= -0.10$, $P < 0.01$.

ample, the slope of the regression of daughter clutch size on mother clutch size is 0.15 in the collared flycatcher (Gustafsson, 1986), and may be higher in other species (reviewed in Boag and van Noordwijk, 1987; but see Gibbs, 1988). However, most of these studies did not control for maternal effects, which may be positive or negative, and hence the genetic contribution to mother–daughter resemblance is uncertain.

Sources of Resemblance

We use a novel combination of experimental and statistical procedures to evaluate several causes of resemblance between mothers and daughters. To begin, we assume that clutch size of an individual female has two components, an additive genetic component and a nongenetic component that hereafter we call "condition." The latter component in turn is made up of both environmental and maternal parts. "Condition" is best thought of as a composite of nongenetic factors affecting clutch size, including nutritional state, level of health, experience, and amount of physiological wear-and-tear. Note that condition has no genetic component by definition; we assume that all genetic influences are mediated through the additive genetic component of clutch size.

Field studies of the collared flycatcher suggest two nongenetic routes by which mothers influence the condition and hence clutch size of daughters. The first is the effect m of mother clutch size on daughter condition, when other influences are held constant. Experiments accumulated over several years reveal that the addition of eggs to

the clutch of a female reduces the mean clutch size of her daughters, whereas removing eggs increases daughter clutch sizes (Fig. 1; this experiment is described in Materials and Methods below). This effect is a "between-generation cost of reproduction" (Stearns, 1989; Gustafsson and Sutherland, 1988).

The second maternal effect (hereafter called M) is the influence of mother condition on daughter condition, when clutch size is held constant. If present, this quantity should be positive: we expect mothers in good condition to produce daughters in good condition, when mother clutch size and genotype are held constant. An experimental measurement of this effect would require that both food levels and clutch size be manipulated, which has not been reported. However, observations indirectly support the presence of the second maternal effect. For example, mother's condition appears to decline with advancing age, as suggested by the decline in her clutch size after her third year of breeding (Gustafsson and Pärt, 1990). The clutch size of daughters similarly declines with mother's age (Fig. 2), suggesting that daughter's condition declines with mother's condition (and hence that a positive M is present). A quantitative estimate of M using degree of resemblance between mothers and daughters is a goal of our study.

The two postulated maternal influences are illustrated in Figure 3. A third path is also shown indicating the additive effects of genes: A daughter inherits half her genetic component of clutch size from her mother, assuming random mating. We use the degree of resemblance between mothers and
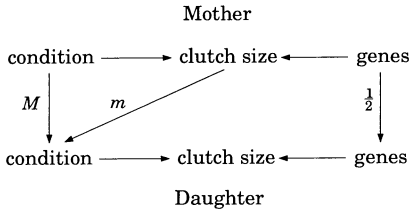
Mother

Daughter

FIG. 3. Genetic and maternal effects on daughter condition and clutch size in daughter's first year of breeding. Arrows connect dependent variables (arrowhead) with independent variables. Path symbols are partial regression coefficients, set to one unless otherwise indicated. M and m are the direct maternal effects.

daughters to estimate the magnitude of the genetic component.

MATERIALS AND METHODS

Field Study

The collared flycatcher was studied from 1980 to 1988 on the island of Gotland, Sweden, where it exists as an isolated population with a remarkably high site fidelity of both adults and young (Gustafsson, 1985; Pärt and Gustafsson, 1989). As a result, the lifetime reproductive success of individuals can be assessed with an accuracy rarely possible in nature (Gustafsson, 1989). The study area consisted of nine woodlands containing more than 900 nest boxes in total. Eight woodlands were deciduous, dominated by oak *Quercus robur* and ash *Fraxinus excelsior,* with a dense understory of hazel *Corylus avelana* and hawthorn *Crategus* spp. The ninth area was in coniferous forest dominated by pine *Pinus sylvestris* and containing some birch *Betula pubescens.*

The species is migratory. Each year, the first males arrive on Gotland in the first week of May and immediately establish territories. The first females arrive one week later on average. The first eggs are laid around 20 May, and most clutches hatch during the first half of June. Broods contain from four to eight young, which normally fledge 14 or 15 days afte.· hatching. Young in all nests have fledged by 15 July. Only one clutch is laid per season, except for a few replacement clutches begun after the first one has failed (not considered here). Individuals usually breed at one year of age, although a small fraction delay breeding until their second year.

All nests in the study were monitored regularly. Laying date, clutch size, hatching date, number of young and number of fledglings in each brood were recorded. Body weight and tarsus length of each young were measured 13 days after hatching, and the bird was then fitted with a uniquely numbered leg band. The number of offspring recruited into the breeding population in subsequent years was determined by catching all breeding pairs within the study area and reading their band numbers. Survival of adults was monitored in the same way. Unbanded immigrant parents were occasionally found, and were captured and banded. The age of these birds (whether 1 year or older) could be determined by plumage.

Clutch Size Experiment

The clutches of 320 collared flycatchers were manipulated during the three years 1983–1985 (Gustafsson and Sutherland, 1988). Clutches having the same hatching date were treated in pairs. In experimental clutches, either one or two randomly selected young were removed from one nest at two days of age and placed in the other nest. In controls, two young were swapped between nests. The number of young added or removed was independent of the original number of eggs laid. Hence, estimates of the maternal effect m (Fig. 1) are unconfounded by other maternal or genetic influences on clutch size. Exchange of young took only a few minutes, since paired nests were always less than five hundred meters apart. Transferred young included hatched, unhatched, and dead individuals. This procedure takes into account variation between nests in mortality of newborn young or eggs, such that the transfer is analogous to moving eggs prior to hatching. By transferring a small number of young we achieved a range of clutch sizes close to the natural range.

Quantitative Genetics

We employed a new procedure to estimate additive genetic variance and maternal effects in a sex-limited trait (clutch size). Our sample sizes were too small to use the typical approach, which is to compare the resemblance between mothers and daughters to that between daughters and grandparents (Falconer, 1981; van Noordwijk et
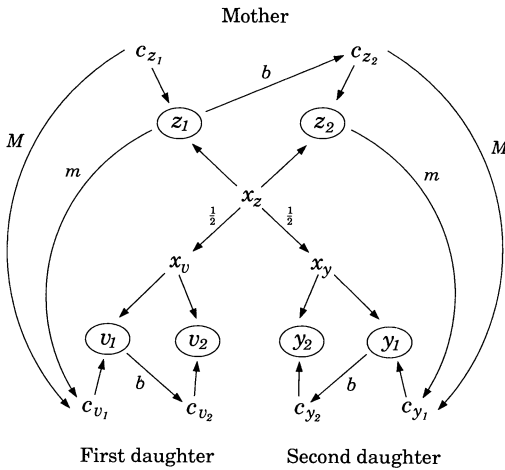
FIG. 4. Sources of resemblance between mother and daughters, z is mother clutch size, v is clutch size of a daughter born in mother's first year of breeding, and y is clutch size of a daughter born in mother's second year of breeding. Subscripts 1 and 2 indicate year of breeding for mother or daughters. c indicates condition, and x is the additive genetic component of clutch size. Arrows connect dependent (arrowhead) with independent variables. Path labels are the partial regression coefficients; these are set to one unless otherwise indicated.
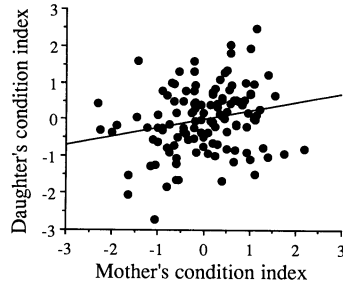

FIG. 5. Condition index of daughters in their first year of breeding and the condition index of their mothers in the year daughter was born. Slope $= 0.26$, $N = 124$, $R^2 = 0.06$, $P < 0.01$.

al., 1981; Janssen et al., 1988) (e.g., we had only 24 grandmother–daughter pairs). Instead, we used the covariances among the clutch sizes of mothers and daughters in their first and second years of breeding (Fig. 4). This procedure was suggested by our finding that clutch size of a female in her first year of breeding was not strongly correlated with that in her second year ($r = 0.28$). This implied that the causes of variation in the second clutch were not identical with those of the first, and that a comparison of the two might allow us to disentangle genetic and maternal causes. Our approach is similar in spirit to the covariance method of Lande and Price (1989).

Six clutch size variables were used in all, as illustrated in Figure 4: mother in her first year of breeding, z_1; mother in her second year of breeding, z_2; "first daughter" (daughter born of a mother's first clutch) in her first (v_1) and second (v_2) years of breeding; and "second daughter" (daughter born of a mother's second clutch) in her first (y_1) and second (y_2) years of breeding. The method could be extended to include also the third and higher clutches of mothers and

daughters, but our sample sizes were too small to warrant the large number of extra equations needed.

We consider that the clutch sizes of a mother (z) in her first and second years of breeding have two components, an additive genetic component x_z, assumed to be the same for both clutches, and a condition component:

$$z_1 = x_z + c_{z_1} \qquad \text{(1a)}$$

$$z_2 = x_z + c_{z_2}. \qquad \text{(1b)}$$

The terms c_{z_1} and c_{z_2} are not independent, because they may have common environmental causes, and because each egg produced by a female in her first year directly reduces condition in her second year (Fig. 1). We let

$$c_{z_2} = bz_1 + \epsilon_{z_2}, \qquad \text{(2)}$$

where ϵ_{z_2} is an environmental deviation. The parameter b is the depression of a mother's clutch size in her second breeding season that results directly from the raising of each egg in her first season. b is the cost of present reproduction to future reproduction, and its magnitude is known from experiments (Gustafsson and Sutherland, 1988; Gustafsson and Pärt, 1990). Because it represents an effect of the phenotype at one age on the phenotype at a later age, b is also an example of an "epigenetic effect" (Cowley and Atchley, 1992). The term c_{z_1} also has two components, one maternal and one environmental, similar to those described below for daughter condition. This formulation assumes that the maternal effects are directly received by a female's first clutch

and not her second. We discuss this assumption in the following section.

The clutch sizes of a "first" daughter (a daughter born of a mother's first clutch) in her first and second year of breeding similarly consist of two components:

$$v_1 = x_v + c_{v_1} \qquad (3a)$$
$$v_2 = x_v + c_{v_2}, \qquad (3b)$$

where x_v is the common genetic component, and c refers to condition. Condition of the first daughter in her first year of breeding has two maternal components (see Fig. 3), one attributable to mother condition and the other to mother clutch size, plus an environmental deviation:

$$c_{v_1} = Mc_{z_1} + mz_1 + \epsilon_{v_1}. \qquad (4a)$$

Condition in her second year of breeding is partly determined by clutch size in her first year:

$$c_{v_2} = bv_1 + \epsilon_{v_2}. \qquad (4b)$$

ϵ_{v_1} may be correlated with ϵ_{v_2}, but neither is correlated with the genetic and maternal components of clutch size.

Analogous components make up clutch sizes of the "second" daughter, daughters born of a mother's second clutch:

$$y_1 = x_y + c_{y_1} \qquad (5a)$$
$$y_2 = x_y + c_{y_2}. \qquad (5b)$$

The condition of a second daughter in her first year of breeding is assumed to be maternally affected only by her mother's clutch size and condition in the year the daughter was born. Hence

$$c_{y_1} = Mc_{z_2} + mz_2 + \epsilon_{y_1}. \qquad (6a)$$

Finally, condition in her second year is influenced by her first clutch size:

$$c_{y_2} = by_1 + \epsilon_{y_2}. \qquad (6b)$$

As above, ϵ_{y_1} and ϵ_{y_2} may be correlated. These relationships are diagrammed in Figure 4. The covariances between the six clutch size variables are given in the Appendix.

We express the additive genetic variance (σ_x^2) in units of total phenotypic variance (σ_z^2): $h^2 = \sigma_x^2/\sigma_z^2$. The quantity h^2 is not strictly "heritability" in the usual sense because the genetic and nongenetic components of clutch

size are correlated when maternal effects are present (Kirkpatrick and Lande, 1989; Appendix), and so their variances do not sum to the phenotypic variance $(\sigma_x^2 + \sigma_c^2 \neq \sigma_z^2)$. Additionally, h^2 does not predict evolutionary response to natural selection when maternal effects are present (Kirkpatrick and Lande, 1989).

Assumptions of the Analysis

We employ standard assumptions of quantitative genetics: effects are linear and additive, genes are autosomal, the population is at evolutionary equilibrium, and covariances between relatives are not affected by natural selection (Lande and Price, 1989). For simplicity, we assume that nonadditive genetic factors affecting clutch size are negligible. However, a nonadditive term could be incorporated in the environmental component of condition. We ignore any possible nongenetic paternal contribution to clutch size, and assume it to be uncorrelated with the mother's contribution. We assume that first and second daughters of the same mother are related as half-sibs, since only 5% of females remate with the same male (Pärt and Gustafsson, 1989, and unpubl. data).

We define m and M to be the maternal effects of mothers on the first clutches produced by their daughters (Fig. 4). Maternal effects on second clutches are mediated only through the first. This assumes that the direct maternal effects have largely decayed by the time a daughter produces her second clutch. An alternative model might add the maternal effects m and M on second clutches also, but this assumes undiminished maternal effects on daughter condition regardless of daughter age, which we regarded as less realistic. For example, Price and Grant (1985) found that maternal effects on offspring morphology in Darwin's finches decayed rapidly as the offspring aged. Maternal effects in insects are also generally strongest on the early developmental stages of offspring (Mousseau and Dingle, 1991). Complete decay is not inevitable—indeed, Figure 1 shows a maternal effect persisting until offspring are a year old. Maternal effects on the weight of laboratory mice also persisted until offspring were adults (63 days; Cowley et al., 1989; Atchley et al., 1991).

A more complex model might include rate of decay of maternal effect as another parameter to be estimated, but this was not possible with our data. However, we have examined the effect of lingering maternal effects on our estimates. For example, if we assumed that the maternal effects on daughters' second year of breeding are half those of the first (rather than zero), then our estimates of M and h^2 were altered, but not qualitatively (the magnitude of M was reduced, and h^2 was greater, by about 20%). The changes were not sufficient to warrant presenting the more complex model.

Estimation

The statistical teasing apart of genetic and maternal effects on clutch size is second-best to a direct experimental approach. Therefore, we rely as much as possible on the results of clutch size manipulations to estimate parameters. This provides the extra benefit of a simplified analysis.

We substituted into the equations (Appendix) the values of m and b estimated from the field experiments (e.g., Fig. 1). We then solved for the remaining quantities M and h^2 using maximum likelihood, using a computer grid search to determine the values of M and h^2 which maximized the probability of obtaining the full set of mother–daughter clutch sizes observed. These probabilities (likelihoods) were calculated assuming that the six mother–daughter variables were approximately multivariate normally distributed.

Statistical significance of the estimates M and h^2 were calculated using a likelihood ratio test (Bickel and Doksum, 1977). For example, let L_1 be the likelihood maximized over all possible values of M and h^2, given the data at hand. Let L_2 be the likelihood maximized over all values of h^2 when $M = 0$. If the null hypothesis of $M = 0$ is correct, then L_1/L_2 should have a χ^2 distribution with one degree of freedom. We used one-tailed tests, since there were strong a priori reasons for predicting that m would be negative, and that h^2 and M would be positive. Support intervals equivalent to 95% confidence intervals were calculated for each trait separately, as the values corresponding to a likelihood one seventh that of the maximum (L_1).

TABLE 1. Estimated sources of resemblance between the clutch sizes of mothers and daughters. M and m are the maternal effects, h^2 is the additive genetic variance divided by the total phenotypic variance, and b is the reduction to a female's second clutch size that results from each additional egg to her first (see Appendix). Support intervals are approximately equivalent to 95% confidence intervals.

Parameter	Estimate	P	Support interval
m	−0.25	0.01	(−0.43, −0.07)
b	−0.25	0.01	(−0.39, −0.11)
M	0.43	<0.001	(0.25, 0.58)
h^2	0.33	0.06	(−0.10, 0.72)

RESULTS

A Negative Maternal Effect

The experiments revealed that the maternal effect m was large and negative: adding a single hatchling to a female's nest reduced the clutch size of her daughters by 0.25 eggs. Thus, to a good approximation, $m = -0.25$. The experiments also provided an estimate of the parameter b, which is the depression in clutch size of a female in her second year of breeding that stems from the rearing of each egg the year before (a "within generation cost of reproduction"; Gustafsson and Sutherland, 1988; Gustafsson and Pärt, 1990). By adding or removing hatchlings, we estimate $b = -0.25$ (Table 1).

Positive Maternal Effects and Additive Genetic Variance

The remaining parameters, M and h^2, were estimated using the measured degree of resemblance between clutch sizes of mothers and daughters. These estimates proved to be large (Table 1). If clutch size and genes are held constant, mother condition had a large positive influence on daughter condition ($M = 0.43$), and hence daughter clutch size. This effect is sufficiently large as to completely offset the negative maternal effect of clutch size alone ($m = -0.25$). The "net" maternal effect of mother condition on daughter condition ($M + m$) should therefore be positive, when additive genetic effects are held constant. Mother and daughter still resembled one another after both maternal effects M and m were accounted for, suggesting the presence of an additive genetic component to clutch size ($h^2 = 0.33$).

However, the estimate was highly variable, and lay on the borderline of statistical significance (one-tailed test; Table 1).

Independent Evidence of M

Of the two maternal effects, m and M (Fig. 3), evidence for the former is most compelling because it is based on direct manipulation of the maternal trait (Fig. 1). Support for the existence of M is indirect and rests on the validity of the statistical model used to calculate it. The relationship between daughter clutch size and mother age is independent circumstantial evidence for M (Fig. 2). Here we describe additional evidence for a significant maternal effect M.

We sought an approximate morphological index of "condition" that could be compared directly between mothers and daughters. As our index we used the residuals from a regression of body mass against tarsus length. Body mass was measured during incubation (i.e., after the last egg was laid), when females gain fat and increase their mass up to 25%. Use of residuals was preferable to body mass alone, as it partly corrects for differences between individuals in structural size. This condition index predicts her prior clutch size (slope = 0.26, R^2 = 0.09, $N = 161$, $P < 0.001$). More telling is that the change in a female's condition index between her first and second year of breeding predicts the change in her clutch size between those same two years (slope = 0.52, $R^2 = 0.25$, $N = 79$, $P < 0.0001$).

It can be shown from the equations provided in the Appendix that a regression of daughter condition c_{v_1} on mother condition c_{z_1} will have a slope approximately equal to $M + m$. As a result, the regression of daughter condition index on mother condition index provides an independent test of whether the net maternal effect $M + m$ is positive, as shown in Table 1 ($M + m = 0.18$). The result revealed a positive slope (= 0.26 ± 0.10 SE, $R^2 = 0.06$, $P = 0.006$), in agreement with our earlier estimates (Fig. 5).

DISCUSSION

There is increasing evidence that parents pass their traits to offspring by both genetic and nongenetic mechanisms (Reznick, 1981; Cheverud, 1984; Price and Grant, 1985;

Roach and Wulff, 1987; Janssen et al., 1988; Mousseau and Dingle, 1991; Larsson and Forslund, 1992). The present study is among the first to evaluate both mechanisms in a wild population. The maternal effects on body condition and clutch size were large, on the order of 0.25 to 0.45 in absolute magnitude. Our study also suggested that clutch size has a moderate additive genetic component, after maternal effects are accounted for, although its magnitude is highly uncertain.

These results indicate that clutch size in the collared flycatcher is an evolutionarily flexible trait and would respond rapidly to a change in natural selection pressures. The response to changing selection would be complex and involve both genetic and maternal components (Kirkpatrick and Lande, 1989). The total magnitude of the response to directional selection is given by the slope of the daughter–mother regression. For example, consider those mothers who were themselves born of grandmother's first clutch. At equilibrium, the regression of their daughter's first clutch size v_1 against the mother's first clutch size z_1 has slope

$$\frac{1}{2}h^2 \frac{(M - 2)(2M - 1)}{2 - (m + M)} + (m + M) \quad (20)$$

(derived from equations 7a and 8). Substituting the values from Table 1 into this equation yields the slope 0.20, a relatively large value. This result is the expected response to selection in the first generation only, as the slope would change in the next (Kirkpatrick and Lande, 1989).

Our results also reveal that the slope of the regression of daughter clutch size on mother clutch size is a poor technique for estimating the additive genetic variance h^2 when maternal effects are present. This is because the slope is almost completely determined by the net maternal effect $m + M$ (the second term of equation 20) over a large range of values for these three parameters. For example, we estimated that $m + M = 0.18$ in the flycatchers (Table 1), which was the much larger of two portions making up our calculated slope (i.e., 0.20 = 0.02 + 0.18; cf. equation 20). This finding means that in other circumstances when the net maternal effect $m + M$ is small or slightly

negative, then a near-zero slope is possible whatever the value of h^2. It follows that a low slope in a regression of daughter clutch size on mother clutch size (e.g., Gibbs, 1988) is not an indication that genetic variance is lacking unless it can be shown that maternal effects are also absent. For the same reasons, a large slope would not necessarily indicate large additive genetic variance. The equations in the Appendix reveal that mother–daughter resemblance in general depends weakly on the additive genetic variance, and this is probably the main cause of high variability in our estimate of h^2 (Table 1). Alternative methods (e.g., resemblance between daughter and paternal grandmother) also tend to yield variable estimates of h^2 (van Noordwijk et al., 1981). Accurately estimating additive genetic variance for clutch size is a challenging future task.

We have assumed that maternal effects are constant, but there are good reasons to predict that they should vary across environments. For example, the negative effect m of mother clutch size on daughter condition may be slight in environments of high food abundance and severe in poor environments. The same may happen between years within a study population. Such variation may have dramatic effects on resemblance between mothers and daughters. For example, variation in m alone should cause the slope of the daughter–mother regression for clutch size (equation 20) to be low in poor environments and high in good environments. Variation in the slope of offspring–parent regressions is often interpreted as indicating variability in additive genetic variance, and hence genotype × environment interaction (Price, 1991; Larsson and Forslund, 1992; Gustafsson and Møller, unpubl. data). However, the pattern could also result from variation in the maternal effects (i.e., a maternal × environment interaction). Distinguishing between these possibilities will require that both genetic and maternal effects be estimated.

The present study shows the value of manipulative experiments in teasing apart the maternal contributions of different phenotypic traits. Estimating specific maternal effects without experiments generally requires measurement of all traits in the parent that maternally affect the offspring trait (Lande

and Price, 1989), an immensely complicated task. Manipulation of isolated parental traits independently of the rest of the phenotype is a valuable, complementary approach (see also Sinervo and McEdward, 1988; Atchley et al., 1991). We obtained our estimate of m by experiment, and suggest the following experiment to test our estimate of M: First, provide supplemental food to part of the population, increasing the condition of mothers. Second, record the increase in mean clutch size of fed birds. Third, remove eggs of experimental birds to reduce clutch sizes to those of control birds (leaving mother's condition unaffected). Finally, measure the clutch sizes of all subsequent daughters. M is estimated by the ratio of the mean increase in daughter clutch size of experimental birds, to the increase in clutch size experienced by their mothers.

LITERATURE CITED

ATCHLEY, W. R., T. LOGSDON, D. E. COWLEY, AND E. J. EISEN. 1991. Uterine effects, epigenetics, and postnatal skeletal development in the mouse. Evolution 45:891–909.

BICKEL, P. J., AND K. A. DOKSUM. 1977. Mathematical Statistics. Holden-Day, San Francisco, CA USA.

BOAG, P. T., AND A. J. VAN NOORDWIJK. 1897. Quantitative genetics, pp. 45–78. In F. Cooke and P. A. Buckley (eds.), Avian Genetics. Academic Press, London, UK.

CHEVERUD, J. M. 1984. Evolution by kin selection: A quantitative genetic model illustrated by maternal performance in mice. Evolution 38:766–777.

COWLEY, D. E., AND W. R. ATCHLEY. 1992. Quantitative genetic models for development, epigenetic selection, and phenotypic evolution. Evolution 46: 495–518.

DAAN, S., C. DIJKSTRA, AND J. M. TINBERGEN. 1990. Family planning in the kestrel (Falco tinnunculus): The ultimate control of covariation of laying date and clutch size. Behaviour 114:83–116.

DRENT, R. H., AND S. DAAN. 1980. The prudent par-

ent. Energetic adjustments in avian breeding. Ardea 76:127–140.

FALCONER, D. S. 1981. Introduction to Quantitative Genetics, 2nd ed. Longman, N.Y., USA.

GIBBS, H. L. 1988. Heritability and selection on clutch size in Darwin's medium ground finches *Geospiza fortis*. Evolution 42:750–762.

GUSTAFSSON, L. 1985. Fitness factors in the collared flycatcher *Ficedula albicollis* Temm. Ph.D. Diss. Uppsala University, Sweden.

———. 1986. Lifetime reproductive success and heritability: Empirical support for Fisher's fundamental theorem. Am. Nat. 128:761–764.

———. 1989. Lifetime reproductive success in the collared flycatcher, pp. 75–89. In I. Newton (ed.), Lifetime Reproduction in Birds. Academic Press, London, UK.

GUSTAFSSON, L., AND T. PÄRT. 1990. Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. Nature 347:279–281.

GUSTAFSSON, L., AND W. SUTHERLAND. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335:813–815.

JANSSEN, G. M., G. DE JONG, E. N. G. JOOSE, AND W. SCHARLOO. 1988. A negative maternal effect in springtails. Evolution 42:828–834.

KIRKPATRICK, M., AND R. LANDE. 1989. The evolution of maternal characters. Evolution 43:485–503.

LACK, D. 1966. Population studies of birds. Oxford University Press, UK.

LANDE, R., AND T. PRICE. 1989. Genetic correlations and maternal effect coefficients obtained from offspring–parent regressions. Genetics 122:915–922.

LARSSON, K., AND P. FORSLUND. 1992. Genetic and social inheritance of body size and egg size in the barnacle goose (*Branta leucopsis*). Evolution 46:235–244.

MOUSSEAU, T. A., AND H. DINGLE. 1991. Maternal effects in insect life histories. Annu. Rev. Entomol. 36:511–534.

PÄRT, T., AND L. GUSTAFSSON. 1989. Causes and consequences of breeding dispersal in the collared flycatcher *Ficedula albicollis*. J. Anim. Ecol. 58:305–320.

PRICE, T. D. 1991. Environmental and genotype-by-environment influences on chick size in the yellow-browned leaf warbler *Phylloscopus inornatus*. Oecologia 86:535–541.

PRICE, T. D., AND P. R. GRANT. 1985. The evolution of ontogeny in Darwin's finches: A quantitative genetic approach. Am. Nat. 125:169–188.

REZNICK, D. 1981. "Grandfather effects": The genetics of offspring size in the mosquitofish *Gambusia affinis*. Evolution 35:941–953.

ROACH, D. A., AND R. D. WULFF. 1987. Maternal effects in plants. Annu. Rev. Ecol. Syst. 18:209–236.

SINERVO, B., AND L. R. McEDWARD. 1988. Developmental consequences of an evolutionary change in egg size: An experimental test. Evolution 42:885–899.

STEARNS, S. C. 1989. Trade-offs in life-history evolution. Funct. Ecol. 3:259–268.

VAN NOORDWIJK, A. J., A. J. VAN BALEN, AND W. SCHARLOO. 1981. Genetic and environmental variation in the clutch size of the great tit *Parus major*. Neth. J. Zool. 31:342–372.

APPENDIX

Here we calculate covariances between the clutch sizes of mothers and daughters in terms of the parameters m, M, b, and h^2. The equations are based on the components outlined in equations 1–6 and as illustrated in Figure 4. To begin, we assume that the variances of the six mother and daughter clutch sizes are equal: $\sigma^2 = \sigma_{z_1}^2 = \sigma_{z_2}^2 = \sigma_{v_1}^2 = \sigma_{v_2}^2 = \sigma_{y_1}^2 = \sigma_{y_2}^2$. We also assume that the covariance between the sizes of first and second clutch is the same in every generation: $\sigma_{1,2} = \text{cov}(z_1, z_2) = \text{cov}(v_1, v_2) = \text{cov}(y_1, y_2)$.

For mothers that were themselves first daughters, using equations (1a), (3a), and (4a) we calculate the covariance between their phenotypic (z_1) and genetic (x_z) values for clutch size to be

$$\text{cov}(z_1, x_z) = h^2\sigma^2 + \frac{mh^2\sigma^2}{2 - (m + M)}. \quad (7a)$$

The first term on the right-hand side of equation (7a) is the additive genetic variance in clutch size. The second term is the covariance between the additive genetic component x_z and the condition component c_{z_1}, which is nonzero when the maternal effect m is present. Similarly, for mothers that were themselves second daughters

$$\text{cov}(z_1, x_z) = h^2\sigma^2 + \frac{h^2\sigma^2(m + b(m + M))}{2 - b(m + M)}. \quad (7b)$$

When $M = 0$ and $b = 0$, equation (7) reduces to Kirkpatrick and Lande's (1989) equation for maternal inheritance of a single trait.

The resemblance between first clutches of mothers and daughters reflect both maternal and genetic sources. For first daughters the resemblance is

$$\text{cov}(z_1, v_1) = (\tfrac{1}{2} - M)\text{cov}(z_1, x_z) + \sigma^2(M + m), \quad (8)$$

and for second daughters it is

$$\text{cov}(z_1, y_1) = (\tfrac{1}{2} - M)\text{cov}(z_1, x_z) + \sigma_{1,2}(M + m). \quad (9)$$

Note that equations (8) and (9) are not identical, and that a mother's resemblance to her first daughter is expected to differ from that to her second daughter. The difference disappears when maternal effects are absent.

A daughter's second clutch does not resemble her mother in the same way that her first clutch does:

$$\text{cov}(z_1, v_2) = \tfrac{1}{2}\text{cov}(z_1, x_z) + b\,\text{cov}(z_1, v_1) \quad (10)$$

$$\text{cov}(z_1, y_2) = \tfrac{1}{2}\text{cov}(z_1, x_z) + b\,\text{cov}(z_1, y_1) \quad (11)$$

[compare equation (10) with equation (8) and equation (11) with equation (9)]. This difference does not dis-

appear even when maternal effects are lacking, unless the cost of reproduction b is also negligible.

The remaining resemblances follow.

$$\text{cov}(z_2, v_1) = \sigma_{1,2}(M + m)$$

$$+ (\tfrac{1}{2} - M)[h^2\sigma^2 + b\, \text{cov}(z_1, x_z)] \qquad (12)$$

$$\text{cov}(z_2, v_2) = \tfrac{1}{2}[h^2\sigma^2 + b\, \text{cov}(z_1, x_z)]$$

$$+ b\, \text{cov}(z_2, v_1) \qquad (13)$$

$$\text{cov}(z_2, y_1) = \sigma^2(M + m)$$

$$+ (\tfrac{1}{2} - M)[h^2\sigma^2 + b\, \text{cov}(z_1, x_z)] \qquad (14)$$

$$\text{cov}(z_2, y_2) = \tfrac{1}{2}[h^2\sigma^2 + b\, \text{cov}(z_1, x_z)]$$

$$+ b\, \text{cov}(z_2, y_1) \qquad (15)$$

$$\text{cov}(v_1, y_1) = \tfrac{1}{2}\text{cov}(z_1, x_z)$$

$$\cdot[m + M(1 - 2m) - 2M^2(b + 1)]$$

$$+ M^2\sigma_{1,2} - \tfrac{1}{2}M(h^2\sigma^2 - 2m\sigma_{1,2})$$

$$+ m\, \text{cov}(z_2, v_1) \qquad (16)$$

$$\text{cov}(v_1, y_2) = b\, \text{cov}(v_1, y_1) + \tfrac{1}{2}\text{cov}(z_1, x_z)(M + m)$$

$$+ \tfrac{1}{4}h^2\sigma^2(1 - 2M) \qquad (17)$$

$$\text{cov}(v_2, y_1) = b\, \text{cov}(v_1, y_1) + \tfrac{1}{2}b\, \text{cov}(z_1, x_z)(M + m)$$

$$+ \tfrac{1}{4}h^2\sigma^2(2m + 1) \qquad (18)$$

$$\text{cov}(v_2, y_2) = b\, \text{cov}(v_1, y_2) + \tfrac{1}{2}b^2\text{cov}(z_1, x_z)(M + m)$$

$$+ \tfrac{1}{4}h^2\sigma^2[b(2m + 1) + 1] \qquad (19)$$