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Individual variation in metabolism and reproduction of *Mus*: are energetics and life history linked?

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Summary

The possibility of functional relationships between energetics and life-history characteristics has been of considerable interest to evolutionary ecologists. Among species of mammals, life-history variables generally are not correlated with mass-independent basal metabolic rate, with the possible exceptions of maximal intrinsic rate of increase, litter size and reproductive effort during lactation. Whether this is generally true at the level of variation among individuals within a population (individual variation) is unclear. Therefore, we tested whether basal or maximal metabolic rates of random-bred female mice *(Mus domesticus)* were correlated with the size of their litters, litter mass, or mean offspring mass. The effects of variation in maternal mass, maternal age, experimental block and duration of fasting (for basal metabolic rate) were removed by calculating residuals from multiple regression equations. Basal and maximal metabolic rate were not significantly correlated with any of the life-history variables we studied. Thus, our results are generally consistent with those from interspecific comparisons of mammals: little evidence suggests necessary associations between metabolic rates and life history.

Key-words: Basal metabolic rate, energetics, individual variation, life history, litter mass, litter size, maximal metabolic rate, *Mus domesticus*, reproduction

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Introduction

Body mass has profound effects on the biology of animals (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Damuth & MacFadden 1990). Interspecifically, body mass and metabolic rate are correlated in a broad range of taxonomic groups including reptiles (Andrews & Pough 1985; Chappell & Ellis 1987), amphibians (Taigen 1983), birds (Bennett & Harvey 1987) and mammals (Taylor *et al.* 1981; Elgar & Harvey 1987; Nagy 1987; McNab 1988). Many life-history variables (e.g. offspring mass, litter mass, developmental rates) are also interspecifically correlated with body mass (Leitch, Hytten & Billewicz 1959; Millar 1977; Blueweiss *et al.* 1978; Western 1979; Stearns 1983; Calder 1984). The mutual dependence of both metabolic rate and life-history variables on body mass results in a correlation between metabolic rate and life-history variables as well.

When variation due to body mass is controlled, however, basal metabolic rate and life-history variables are generally uncorrelated (Harvey, Pagel & Rees 1991, but cf. Thompson 1991). Basal metabolic rate (BMR), independent of body mass, and maximal intrinsic rate of increase (r_{max}) are correlated (Hennemann 1983, 1984; Schmitz & Lavigne 1984), but how this relationship is affected by non-independence among the taxa studied is unknown (Felsenstein 1985; Pagel & Harvey 1988; Harvey & Pagel 1991; Martins & Garland 1991). Harvey *et al.* (1991) reported that litter size (number of offspring per litter) was the only one of 22 life-history variables they examined that was significantly correlated with basal metabolic rate after controlling for body mass. They suggested this was simply a chance effect.

The dependence of both life history and metabolism on body mass has led to a search for links between energy use (metabolic rate) and life history (e.g. see Sacher & Duffy 1979; McNab 1980, 1986; Derting & McClure 1989). One hypothesis is that a correlation between metabolic rate and life history results from consequences of resource allocation. The principle of allocation states that available energy is partitioned between maintenance, growth and reproduction (Gadgil & Bossert 1970). Thus increased allocation to one use (e.g. maintenance) reduces energy available for other uses (e.g. growth and reproduction), if total energy is fixed. McNab (1980) concluded that there was little interspecific evidence for a trade-off in allocation of energy between maintenance and reproduction in mammals. He proposed instead that animals with high rates of

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metabolism will actually have high rates of biosynthesis and, consequently, grow faster and synthesize tissue in the form of offspring more rapidly. An implicit assumption of this argument is that animals with higher metabolic rates also have higher metabolizable energy intake, so that the resources needed to fuel greater rates of biosynthesis are actually available. Irrespective of any ineluctable functional, mechanistic or physiological connections, a third possibility is that energetic and life-history traits might be associated simply because (correlated) selection pressures have favoured particular combinations of traits (cf. the *r*- and *K*-selection paradigm).

The foregoing examples indicate that the relationships between metabolic rate, body size, and life history of mammals are complex, and that elucidating the causes of these relations can be difficult (Elgar & Harvey 1987; McNab 1988; Pagel & Harvey 1988; Derting & McClure 1989). In addition to the possible confounding effects of body mass, another concern is distinguishing between functional relationships at different levels of variation [i.e. within a population (individual variation), among populations or experimental groups of a single species, and among species]. Relationships may vary among the different levels of variation (Lande 1979, 1985; Cheverud 1982; Zeng 1988; Earle & Lavigne 1990; Garland & Adolph 1991). In this paper, we examine the relationships between body mass, metabolic rate and reproduction at the level of individual variation. We test whether metabolic rate is correlated with variation in litter size, mean offspring mass, or total litter mass. Our objective is to examine the phenotypic relationship between metabolism and life-history variables and to compare our results with recent interspecific analyses.

Materials and methods

ANIMAL HUSBANDRY, MEASUREMENT CHRONOLOGY AND BREEDING DESIGN

We studied the random-bred HSD/ICR strain of mice *(Mus domesticus)* obtained from Harlan Sprague Dawley, Inc., Indianapolis, Indiana. The physiology, morphology and life history of this strain have been extensively studied (Robeson, Eisen & Leatherwood 1981; Cheverud *et al.* 1983; Riska, Atchley & Rutledge 1984; Eisen 1986). We obtained data from a total of five groups of mice each treated as a separate block (see Statistical analyses). Each group consisted of four males and up to 20 females. Mice were weaned at 19 days of age and were shipped to Madison from Indianapolis immediately thereafter. Each individual was specified to be from a different family.

Mice were housed in standard clear plastic cages (27 cm long, 17 cm wide, 12·5 cm deep) with metal or wire tops and wood shavings as bedding. Males were placed in individual cages and females were placed in groups of four or five per cage. Mice had unrestricted access to food (Purina Rodent Chow, High-Energy Formula) except during fasting prior to measurements of BMR and during measurements. Water was available *ad libitum* except while measurements were being made. Room temperature was maintained at 23 °C with a 12-h light/dark cycle.

When the mice reached 32 days of age, BMR measurements were initiated. BMR measurements were completed by the time mice were 43 days old. $\dot{V}O_2$max was measured at least 2 days after BMR was measured, but measurements were completed by the time mice were 47 days old. Due to technical difficulties $\dot{V}O_2$max was not measured for the first block.

Within 3 days of finishing the foregoing measurements, mice were paired for breeding. Each male was harem mated to four or five randomly selected females. The harems (including the males) were left together for 8–11 days, at which time the males were removed and the females were placed in individual cages. Pregnant females were monitored daily until parturition. At *c.* 18.00 h on the day of parturition, the number of offspring was counted, and each offspring and the dam were weighed to the nearest 0·01 g.

METABOLIC MEASUREMENTS

BMR is thought to be indicative of the minimal maintenance cost for a homeothermic animal. BMR of post-absorptive animals was measured once at 32 °C (within the thermal neutral zone, Lacy & Lynch 1979) for each animal. Mice were fasted overnight and placed in glass metabolism chambers the next morning. The chambers were part of an open-circuit respirometry system. Up to seven mice were monitored simultaneously. Each mouse and a control chamber received dry air at 200 $cm^3\ min^{-1}$ from upstream thermal mass flow controllers (Sierra Instruments, Inc., Monterey, California, Side=Track Model 844). Water and CO_2 were removed from the excurrent air with Drierite and Ascarite, respectively. Excurrent air from each chamber was monitored every 5 s for at least 7·5 min of each hour (more if fewer than seven mice were being measured) by an Applied Electrochemistry S-3A/II oxygen analyser (Ametek, Pittsburgh, Pennsylvania) interfaced to a microcomputer. Air was diverted by an automated system with solenoid valves under programmed control. We calculated $\dot{V}O_2$ for the last 5 min before switching to the next chamber using the appropriate equation given by Hill (1972). With the flow rate and chamber volumes we used, this protocol ensured clearing of the respirometry system downstream of the metabolism chamber before the start of the 5-min interval. The data analysis program corrected for drift in the control

channel (baseline) using linear regression to calculate predicted baseline values throughout the course of the intervening sampling. The analysis program calculated the lowest and second lowest 5-min intervals of oxygen consumption of the day for each mouse. We used the lowest value in all calculations. The correlation of the lowest and second lowest value was used to assess repeatability (cf. van Berkum *et al.* 1989).

Maximal oxygen consumption ($\dot{V}O_2$max), the upper limit to sustained aerobic activity, was measured via an increasing step test during graded treadmill exercise. Mice were placed in a small chamber on the treadmill at an initial speed of $1{\cdot}0\,km\,h^{-1}$ and speed was increased $0{\cdot}5\,km\,h^{-1}$ every 2 min up to a maximum of $4{\cdot}5\,km\,h^{-1}$. None of the mice could run at $4{\cdot}5\,km\,h^{-1}$ for 2 min. In a larger study, we found that in only four runs out of 650 could mice run at $4{\cdot}5\,km\,h^{-1}$ for even a few seconds (J.P. Hayes, T. Garland & M. R. Dohm, unpublished data). The tread belt was stopped when the mouse was no longer able to maintain pace. $\dot{V}O_2$ was recorded throughout the run and continued to be recorded until about 2 min after the belt was stopped. A brief elevation in oxygen consumption was evident after every run. All mice reached a tread speed of at least $2{\cdot}0\,km\,h^{-1}$. $\dot{V}O_2$max measured by similar techniques is highly repeatable in rats (Bedford *et al.* 1979; Divine, Patch & Brooks 1980).

Oxygen consumption during $\dot{V}O_2$max determinations was monitored with an open circuit respirometry system. Air was drawn from the chamber through a thermal mass flow controller at 2500 $cm^3\,min^{-1}$. This flow rate ensured rapid chamber washout. We also determined the effective volume of the system (540 ml) and made 'instantaneous' corrections for chamber washout (Bartholomew, Vleck & Vleck 1981), since the standard equations given in Withers (1977) are for use under steady state conditions. With the rapid washout of this system, the instantaneous correction was relatively minor, resulting in $\dot{V}O_2$max estimates that were only slightly higher than steady state values (see Results). Oxygen concentration in the excurrent air was sampled every second using an Applied Electrochemistry S-3A/II oxygen analyser interfaced to a computer. Water and CO_2 were removed upstream of both the mass flow controller and the oxygen sensor using Drierite and Ascarite, respectively. $\dot{V}O_2$max was the highest 1-min period of any run. $\dot{V}O_2$max was measured on each of 2 consecutive days and the higher of the two values was used in our analyses. Our protocol produced repeatable $\dot{V}O_2$max values (see Results).

STATISTICAL ANALYSES

Relationships between variables were examined using Pearson product–moment correlations (hereafter correlation), simple linear and multiple least squares regression, and principal components analysis. Several variables were transformed to improve normality and/or homoscedasticity. To control for extraneous factors that might obscure the underlying relationships we wished to examine, we worked primarily with residuals from multiple regression equations. Classification variables, such as block and sex, were coded as dummy variables (0 or 1). Only independent variables significant at $P < 0{\cdot}05$ were retained in multiple regression equations prior to computation of residuals. Means are reported ±1 SD.

Results

AEROBIC METABOLIC RATES

Mean basal metabolic rate (BMR) was $38{\cdot}5\,ml\,O_2\,h^{-1}$ for 74 dams with a mean mass of 20·7 g (Table 1). BMR was significantly correlated ($r=0{\cdot}484$, $n=74$, $P<0{\cdot}001$) with body mass (Fig. 1). Body mass, age and fasting period all explained significant amounts of the variation in BMR (Fig. 2 and Table 2). (Fasting period was computed as the time from when food was removed to the midpoint of the 5-min interval for BMR; it averaged 21·2±1·74 h, range 16·7–24·0 h.) As a measure of the repeatability of BMR, the

Table 1. Descriptive statistics for random-bred ICR house mice

Variable	*n*	Mean	SD	Range	CV%
Litter size	78	9·44	2·40	2–16	25·5
Mean offspring mass (g)	78	1·56	0·148	1·30–2·00	9·5
Total litter mass (g)	78	14·5	3·68	3·89–25·6	25·4
Mass after parturition (g)	78	33·5	3·20	26·6–41·3	9·6
Age at birth (days)	78	66·8	3·71	62–76	5·6
BMR (ml O_2 h^{-1})	74	38·5	6·58	12·5–55·5	17·1
Mass at BMR (g)	74	20·7	2·23	16·2–27·1	10·8
Age at BMR (days)	74	36·4	3·30	32–43	9·1
$\dot{V}O_2$max (ml O_2 h^{-1})	61	248·0	34·8	183–323	14·0
Mass at $\dot{V}O_2$max (g)	61	22·2	2·28	18·0–28·9	10·3
Age at $\dot{V}O_2$max (days)	61	40·7	3·12	38–47	7·7

SD, standard deviation; CV%, coefficient of variation.

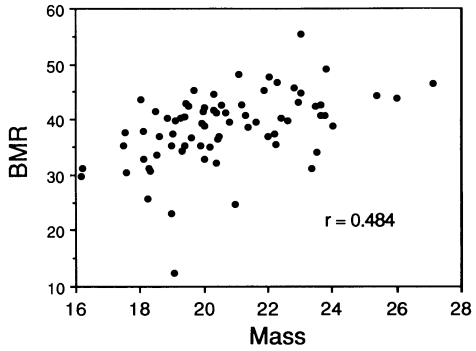

Fig. 1. Scatter plot of the correlation of BMR and body mass (r=0·484, P<0·001).

correlation between the lowest (used as BMR) and the second lowest 5-min intervals of oxygen consumption was 0·929 (n=74, P<0·001).

Mean $\dot{V}O_2$max was 248 ml $O_2 h^{-1}$ for dams with a mean mass of 22·2 g (Table 1). This 'instantaneous' $\dot{V}O_2$max was 4·4±1·91% (range=0·9–9·5%) higher than if $\dot{V}O_2$max was calculated using the steady state equation. The correlation between instantaneous and steady state values was 0·983. Instantaneous $\dot{V}O_2$max was significantly repeatable between trials (r=0·787, n=61, P<0·001). Log $\dot{V}O_2$max was positively correlated (r=0·785, P<0·001) with body mass (Fig. 3). Body mass, age and block explained significant amounts of the variation in log $\dot{V}O_2$max (Table 2).

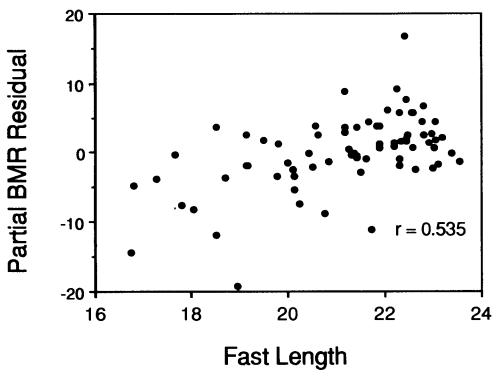

Fig. 2. Partial residual BMR (adjusted for dam mass and dam age) plotted *vs* fast length (the time from when food was removed to the midpoint of the 5-min interval for BMR). Note the partial correlation is significant (P<0·05) and positive.

LIFE HISTORY

Of 94 dams paired with males, 78 gave birth. χ^2-tests and a hierarchical log–linear model indicated that whether a dam gave birth did not depend on how many other dams were paired with the sire (n=4 or 5) or on the length of time dams were left with sires (range 8–11 days). Stepwise multiple regression analyses with dummy variables also indicated that whether a dam gave birth was not related to her body mass, BMR or $\dot{V}O_2$max.

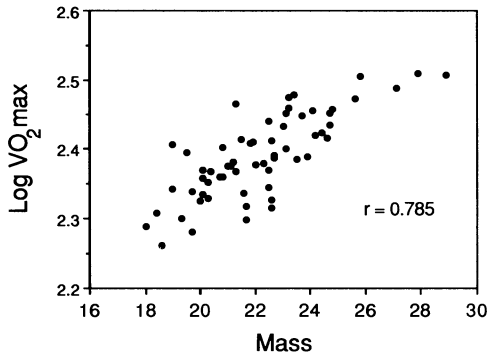

Fig. 3. Scatter plot of the correlation of log $\dot{V}O_2$max and body mass (r=0·785, P<0·001).

Litter size ranged from two to 16 with 80% of all litters between eight and 12 (Fig. 4). Mean litter size was 9·46 (Table 1). Individual offspring ranged in mass from 1·02 and 2·12 g. Mean offspring mass was 1·56 g (range 1·30–2·00 g). Total litter mass at birth varied from 3·89 g for the litter of two to 25·63 for the litter of 16. Multiple regression indicated that dam mass and age at birth control accounted for significant amounts of the variation in both litter size and total litter mass (Table 2).

CORRELATIONS

Bivariate correlations among life-history variables indicated that total litter mass was correlated with dam mass and dam age, that litter size was correlated with dam mass, dam age and litter mass, and that mean offspring mass was negatively correlated with litter size (Table 3). The correlation between litter

Table 2. Signficant (P<0·05) covariates of life-history and metabolic rate characters for dams. Values are partial r^2 (%).

Variable	n	Body mass	Age*	Block	Multiple r^2
Litter size	78	29·4	3·9	—	33·3%
Mean offspring mass	78	—	—	—	0
Total litter mass	78	29·2	8·2	—	37·4%
BMR	74	18·1	5·1	—	51·6%†
$\dot{V}O_2$max	61	61·6	9·2	4·6	75·4%

*Age squared never added significantly to prediction of any dependent variable.
†Fasting period (see text) also explained 28·4% of the variation in BMR.

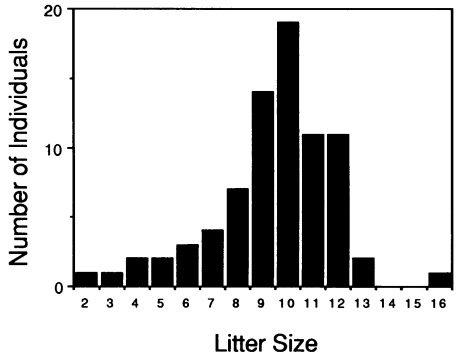

Fig. 4. Histogram of litter sizes for 78 litters of *Mus domesticus*.

size and mean offspring mass persists when variation associated with dam body mass and age is removed (Table 4). None of the three residual life-history characters showed any significant correlation with either basal metabolic rate or maximal oxygen consumption (Figs. 5–7 and Table 4). Multiple regression analyses of residual characters indicated that forcing both BMR and $\dot{V}O_2$ max into a model still did not result in any significant predictive ability.

Principal components analysis was also performed on the correlation matrix of Table 4. When litter size and mean offspring mass are considered with the two metabolic variables, the conclusions based on bivariate patterns are confirmed (Table 5). The major axis of variation reflects a trade-off between litter size (number) and mean offspring mass, and life-history variables appear independent of variation in BMR or $\dot{V}O_2$max. When total litter mass and the two metabolic variables are considered (Table 6), principal components analysis indicated no strong associations between any of the three variables. Each of the component axes explained a similar amount of total variation, which is evidence that there are no strong patterns of covariation between metabolic and life-history variables.

Discussion

The metabolic data we obtained are in good agreement with previous reports of BMR and $\dot{V}O_2$max for *Mus*. The mean basal metabolic rate that we measured was 38·5 ml O_2 h^{-1} for mice averaging 20·7 g. Lynch *et al.* (1976) and Lacy & Lynch (1979) found very similar values (43·1–63·3 ml O_2 h^{-1}) for mice weighing (20·5–28·3 g). We found a mean $\dot{V}O_2$max of 248 ml O_2 h^{-1} for mice with a mean mass of 22·2 g. Hart (1950, 1952) and Pasquis, Lacaisse & Dejours (1970) found slightly higher values for $\dot{V}O_2$max elicited by mice running in the cold at lower tread speeds [see also Rosenmann & Morrison (1974) for data from He-O_2 cold exposure].

The mice we studied varied substantially in the number of offspring (two to 16 pups) and the total mass of offspring in a litter (3·89–25·6 g). The range of variation in the mean mass of offspring (1·30–2·00 g) was much smaller. Given that the variation in mean offspring mass is small and that litter mass is the product of body mass and mean offspring mass, the strong positive correlation (r=0·944) between litter size and litter mass is not surprising (Table 3). The negative correlation (r=−0·418) between mean offspring mass and litter size (Table 3) is consistent with the pattern shown for *Mus* (Parkes 1926), other rodents (Hamilton 1962; Cameron 1973; Millar 1978; Myers & Masters 1983), and other mammals (Clutton-Brock, Albon & Guinness 1988).

Dam mass after parturition accounted for 29·4 and

Table 3. Pearson product–moment correlations between life-history characters (n = 78)

	Litter size	Mean offspring mass	Total litter mass	Maternal mass	Maternal age
Litter size	1	−0·418	0·944	0·542	0·312
Mean offspring mass		1	−0·118	−0·121	0·134
Total litter mass			1	0·540	0·398
Maternal mass				1	0·220
Maternal age					1

Table 4. Pearson product–moment correlations between life-history and metabolic rate characters, based on residuals from multiple regression equations (effects of body mass, age and block removed). Sample sizes are shown in parentheses

	Litter size	Mean offspring mass	Total litter mass	BMR	$\dot{V}O_2$max
Litter size	1	−0·471 (78)	0·920 (78)	0·134 (74)	0·098 (61)
Mean offspring mass		1	−0·127 (78)	0·062 (74)	−0·164 (61)
Total litter mass			1	0·175 (74)	0·046 (61)
BMR				1	−0·069 (60)
$\dot{V}O_2$max					1

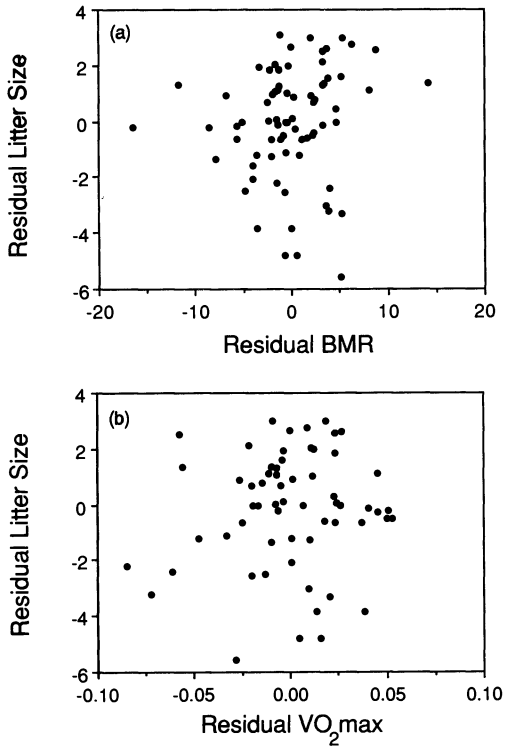

Fig. 5. Residual variation in litter size plotted *vs* residual variation in (a) BMR and (b) $\dot{V}O_2$ max. Neither Pearson product moment correlation was significant ($r=0{\cdot}134$ and $r=0{\cdot}098$, respectively).

29·2% of the variation in both litter size and total litter mass, but dam mass and mean offspring mass were not significantly correlated. A correlation of dam mass with litter size is commonly found in intraspecific studies (Millar 1978, 1983; Myers & Masters 1983; Boag & Boonstra 1988; Earle & Lavigne 1990), although Kenagy *et al.* (1990) reported a positive ($r=0{\cdot}40$) but non-significant correlation between maternal mass and litter size in golden-mantled ground squirrels *(Spermophilus saturatus)*. Earle & Lavigne (1990) also found a significant intraspecific correlation between maternal mass and total litter mass in *Peromyscus maniculatus*.

CORRELATIONS OF LIFE HISTORY AND ENERGETICS

The question of primary interest in this study is whether individual variation in metabolic rates within *Mus* is correlated with variation in life-history traits. We found no evidence that residual variation in metabolic rates was correlated with residual variation in litter size, litter mass, or mean offspring mass (Figs. 5–7 and Table 4). Principal components analysis also indicated little covariation between metabolic and life-history variables.

The literature on life history and metabolism in mammals is extensive, but largely it does not address correlations at the level of individual variation. In one study of individual variation, Earle & Lavigne (1990) found no correlation between maternal resting metabolic rate and litter size, litter mass, or inter-litter interval among individuals in three populations of *Peromyscus maniculatus*. In a comparison of inbred strains of *Mus,* Sacher & Duffy (1979)

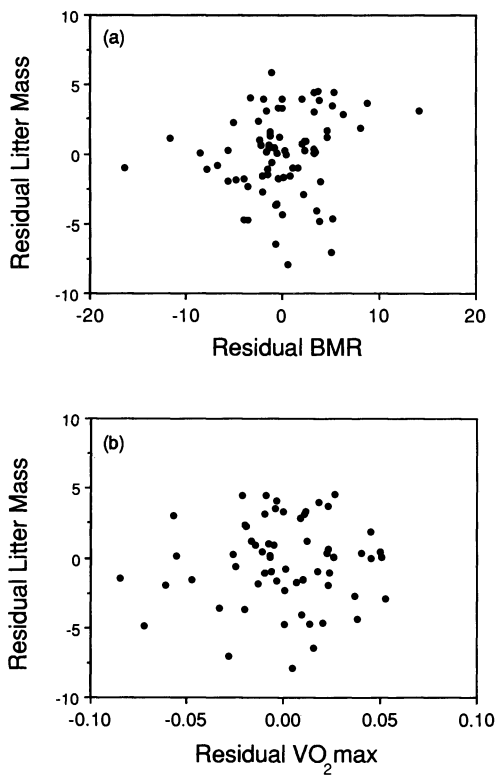

Fig. 6. Residual variation in total litter mass plotted *vs* residual variation in (a) BMR and (b) $\dot{V}O_2$max. Neither Pearson product moment correlation was significant ($r=0{\cdot}175$ and $r=0{\cdot}046$, respectively).

Table 5. Principal components analysis of pairwise correlations of residual characters (from Table 3). Values are component correlations of original variables with principal components

Variable	PCI	PCII	PCIII	PCIV
Litter size	0·82	0·28	−0·14	0·48
Mean offspring mass	−0·84	0·09	0·26	0·48
BMR	0·06	0·86	0·47	−0·18
$\dot{V}O_2$ max	0·40	−0·51	0·76	0·04
Eigenvalue	1·54	1·09	0·88	0·49
% of variance explained	38·4	27·3	22·1	12·2
Cumulative % explained	38·4	65·7	87·8	100·0

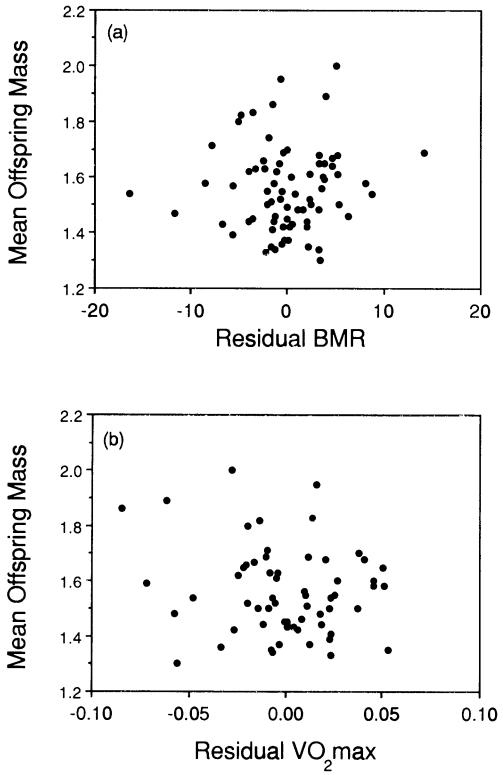

Fig. 7. Residual variation in mean offspring mass plotted *vs* residual variation in (a) BMR and (b) $\dot{V}O_2max$. Neither Pearson product moment correlation was significant ($r=0{\cdot}062$ and $r=-0{\cdot}164$, respectively).

reported a significant negative relationship between metabolism and life-span, but they did not factor out the effects of body mass. Perrigo (1987) showed that *Mus* dams reduce litter size when required to work harder to obtain food, but despite intensive studies of *Mus* by many workers there are no data on the correlation of BMR or $\dot{V}O_2max$ and litter size or litter mass (cf. Bronson 1979; Brien *et al.* 1984; Bronson & Perrigo 1987; Barnett & Dickson 1989). Across populations of cotton rats *(Sigmodon hispidus)*, Derting & McClure (1989) found that the energy dams invested in litters was not correlated with basal metabolic rate.

By manipulating 'basal' metabolic rate with thyroxine and also manipulating food supply, Derting (1989) found that metabolic rates of individual cotton rats affected their growth rates. For juvenile cotton rats on *ad libitum* diets, individuals implanted with thyroxine grew faster than controls. This supports McNab's (1980) hypothesis that metabolic rates are positively correlated with growth and reproduction because of their association with rates of biosynthesis. Conversely, on a food-restricted diet, individuals with thyroxine implants had severely restricted growth compared to controls. This is what would be predicted from the principle of allocation [i.e. energy used for maintenance is not available for growth and reproduction (Gadgil & Bossert 1970)]. Derting's results clearly illustrate the importance of changing rates of energy acquisition on the relationship between metabolic rates and life-history characteristics. The principle of allocation and McNab's (1980) biosynthetic hypothesis are not mutually exclusive. The principle of allocation must hold and any apparent conflict between the two comes from ignoring changes in the size of the available resource pool. Conclusive support for McNab's (1980) hypothesis awaits further confirmation of a correlation between resting metabolic rate and anabolic and/or resource acquisition capacities (cf. Thompson 1991).

INDIVIDUAL *VS* INTERSPECIFIC STUDIES

Overall, metabolic rate and isolated life-history variables do not appear to be strongly related at either the individual or interspecific level. Litter size is significantly interspecifically correlated with mass-independent metabolism, but this is probably the result of chance (Harvey *et al.* 1991). Neither total litter mass nor individual offspring mass was correlated with metabolic rate interspecifically (Harvey *et al.* 1991) or individually (this study). Hennemann (1983, 1984) and Schmitz & Lavigne (1984) have reported significant correlations between r_{max} and metabolic rate. It will be of great interest to learn whether more extensive data sets with rigorous estimates of r_{max} show a similar correlation when controls for the lack of independence of taxa are applied (Felsenstein 1985; Harvey & Pagel 1991).

Much remains to be learned about the relationship (or lack thereof) between metabolism and life history at both the individual and interspecific levels. More

Table 6. Principal components analysis of pairwise correlations of residual characters (from Table 3). Values are component correlations of original variables with principal components

Variable	PCI	PCII	PCIII
Total litter mass	0·74	0·34	−0·58
BMR	0·78	−0·19	0·60
$\dot{V}O_2max$	−0·11	0·94	0·33
Eigenvalue	1·18	1·03	0·79
% of variance explained	39·2	34·3	26·4
Cumulative % explained	39·2	73·6	100·0

integrated measures of life history (e.g. net reproductive rate, r_{max}) may show significant correlations even if isolated life-history characters do not. Correlations may more likely be found, when energetically based measures of life history (e.g. reproductive effort) are studied (cf. Thompson 1991). For example, resting or maximal metabolic rates may not correlate with litter mass, but the amount of energy used to produce a litter may. Variation in metabolism may also be more closely linked to growth than to reproduction as is perhaps suggested by the relationship between basal metabolic rate and whole-body protein metabolism (Waterlow & Millward 1989).

Correlations between life history and metabolic rate may or may not correspond at the individual and interspecific levels. If biosynthetic rates are correlated with maintenance metabolic rates (McNab 1980), the correlations may be influenced by differences in the ability to acquire energy resources in relation to metabolism. For example, within a population, individuals with higher rates of biosynthesis may not be able to utilize their capacities for growth and reproduction because they are unable to increase their total energy assimilation (for either physiological or ecological reasons). Because total energy assimilation is fixed they cannot accommodate the increased maintenance costs and greater allocations to growth and reproduction. If the ability to obtain energy is not correlated with resting metabolic rate, then the principle of allocation dictates that there should be a negative correlation between resting metabolic rate and allocation to growth and reproduction. Individuals using more energy for maintenance will have less energy for growth and reproduction. If individuals with high rates of biosynthesis could increase energy assimilation to some degree this might partially compensate for the increased maintenance requirement. This might result in no correlation or a weak correlation between metabolism and life-history variables. Across species, however, natural selection might have resulted in not only higher metabolic rates, but also a greater ability to acquire energy resources. Hence, differences between individual and interspecific correlations might reflect an evolutionary fine tuning of the ability to acquire energy resources relative to metabolic rate. This would allow species with higher maintenance expenditures to have higher rates of reproduction without violating the principle of allocation, because they increase their total energy intake (cf. McNab 1986).

Finally, there is no reason to expect that individual and interspecific patterns of variation must be similar (Atchley & Rutledge 1980; Cheverud 1982; Lande 1979, 1985; Zeng 1988). The relationship between the two has long been a subject of interest (Huxley 1932; Simpson 1953; Gould 1977), but the connection between them has been clarified only recently by the application of quantitative genetic methods (Lande 1979, 1982, 1985). According to Lande's (1979) model, selection on one of a pair of correlated traits is expected to result in an evolutionary (interspecific) correlation similar to an individual correlation only if the genetic and phenotypic correlations are similar. Dissimilar phenotypic and genetic correlations are one of several reasons that individual and interspecific correlations may differ (Lande 1979, 1985; Turelli 1988; Zeng 1988; Barton & Turelli 1989). Zeng's (1988) analyses indicate that the evolution of correlated characters is dependent on genetic correlations in the short term, but over the long-term fitness functions for stabilizing and directional selection are more important in determining correlations. In short, individual and interspecific correlations need not correspond.

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