Food Quality, Heterozygosity, and Fitness Correlates in Peromyscus polionotus
Author(s): William R. Teska, Michael H. Smith, James M. Novak
Source: *Evolution*, Vol. 44, No. 5 (Aug., 1990), pp. 1318-1325
Published by: Society for the Study of Evolution
Stable URL: http://www.jstor.org/stable/2409291
Accessed: 13/01/2011 15:46

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=ssevol.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Society for the Study of Evolution is collaborating with JSTOR to digitize, preserve and extend access to *Evolution.*

http://www.jstor.org

Evolution, 44(5), 1990, pp. 1318–1325

FOOD QUALITY, HETEROZYGOSITY, AND FITNESS CORRELATES IN *PEROMYSCUS POLIONOTUS*

WILLIAM R. TESKA,
Department of Biology, Furman University, Greenville, SC 29613 USA

MICHAEL H. SMITH,
Department of Zoology, University of Georgia, Athens, GA 30602 USA, and Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801 USA

AND

JAMES M. NOVAK
Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801 USA

Abstract.—Oldfield mice (*Peromyscus polionotus*) that are more heterozygous utilize food and maintain body weight under varying degrees of dietary stress better than their less heterozygous counterparts. Mice were collected in southern Florida and fed diets of three qualities. During each dietary treatment, body weight, amount of food eaten, amount of food absorbed, and feeding efficiency were determined. Body weights for all mice decreased during the experiment. More heterozygous mice maintained their weight better during periods of dietary stress than those that were less heterozygous. Mice with different levels of genetic variability had essentially the same mean feeding efficiency with high quality diets. Mice with high heterozygosities maintained the same efficiency with low quality diets, but those with lower heterozygosities had decreased feeding efficiencies. A slight increase in available energy for mice of different heterozygosities can dramatically change fitness correlated characters, such as growth rates, body weights, energy stores, and reproductive rates.

Received January 10, 1989. Accepted December 21, 1989.

Genetic variability, estimated from protein polymorphisms and expressed as multilocus or allozyme heterozygosity, is frequently correlated with variation in characteristics related to secondary productivity (Mitton and Grant, 1984). Heterozygosity is associated with a number of attributes of individuals, including reproductive rate (Smith et al., 1975), developmental stability (Palmer and Strobeck, 1986), behavior (Garten, 1976, 1977), growth rates (Garton, 1984), body size (Cothran et al., 1983), oxygen consumption (Mitton et al., 1986) and fat utilization (Cothran et al., 1987). Because variation in these attributes influences survivorship and reproductive success, individual fitness probably varies with heterozygosity.

Even if relationships between heterozygosity and fitness correlated characters exist, they may not always be detectable (Mitton and Grant, 1984; Zouros and Foltz, 1987). Mitton and Grant (1984) suggest that the association between heterozygosity and individual characteristics should be strongest when the characteristics affect fitness. Furthermore, they hypothesize that such relationships are more likely to result in an advantage during stress than during optimal environmental conditions. Therefore, a link between heterozygosity and those characters closely related to fitness may not be observed in favorable environments, such as in the laboratory. Other reasons for failing to observe heterozygosity correlates are that too few loci have been studied to give relative measures of genetic variability, and some organisms exhibit low levels of genetic variability, which makes such correlations difficult. Our study was designed to compensate for these problems.

Relationships between heterozygosity and behavior, body size, and reproduction have been established for oldfield mice (*Peromyscus polionotus*) (Smith et al., 1975; Garten, 1976, 1977), a species characterized by high genetic variability. Heterozygosity in *P. polionotus* increases from South Carolina to south Florida (Selander et al., 1971). A positive linear relationship exists between heterozygosity and reproductive rate across this same area (Smith et al., 1975). Garten (1976) also observed a positive relationship between mean body weight of males and their heterozygosity. Social dominance and competitive ability were positively corre-

lated with body weight. More heterozygous *P. polionotus* show higher levels of exploratory behavior than those with lower heterozygosity (Garten, 1977). Exploratory behavior may be advantageous, especially when food is scarce, because prior experience may facilitate the ability of mice to locate food. This ability and that of efficiently handling food of various qualities are important determinants of fitness.

Experiments are needed to test hypotheses concerning relationships among heterozygosity and fitness correlated characters. Heterozygosity might be correlated with a series of such characteristics if it altered the amount of food ingested or absorbed. Small changes in food intake could dramatically affect characters influenced by metabolic processes and productivity (growth and reproduction) and thus overall fitness. Our purpose was to determine whether *P. polionotus* that are more heterozygous utilize food and maintain body weight, under varying degrees of dietary stress, better than their less heterozygous counterparts.

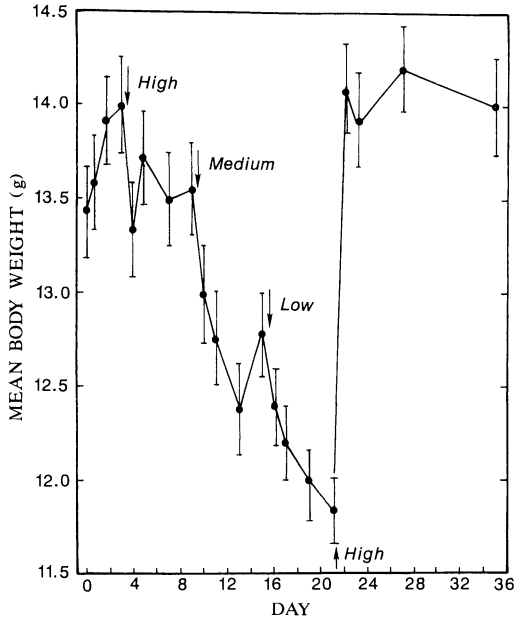

FIG. 1. Mean body weight for mice ($N = 39$) during the experiment. The commencement of dietary treatments, high, medium and low, and a return to high are indicated by arrows. The bars above and below each value represent one standard error.

MATERIALS AND METHODS

Adult male *P. polionotus* ($N = 39$) were collected from Polk and Highlands Co., FL on 13 and 14 July 1985 by digging of burrows and capturing by hand. All mice were obtained from separate burrows to minimize the possibility of collecting siblings. Only males were used to avoid sex-related differences associated with the female reproductive cycle. They were returned to the laboratory, housed individually and fed laboratory chow. The mice were weighed on 16 July, day 0 of the experiment (Fig. 1). After four days (day three of the experiment), the first experimental treatment was applied. Each mouse was sequentially fed diets of three qualities: high, medium, and low. Each diet was fed for a six-day treatment period, and each period was divided into two segments. The first segment lasted for two days and was designated as an acclimation period. The second consisted of four days and served as the measurement period. Food eaten, food absorbed, and feces produced were measured midway and at the end of each measurement period. Amount of food absorbed was calculated by subtraction of egested from ingested amounts of dry matter.

Food quality was varied by the percent of dry straw in the diet. Powdered diets were prepared and thoroughly blended by grinding Purina® rodent laboratory chow (#5001) and locally grown winter wheat straw three times in a Wiley mill using double sieves (2 mm and 1 mm). High, medium, and low quality diets were 0%, 25%, and 50% straw, respectively.

Caloric content of food eaten and of feces produced were determined using a microbomb calorimeter with a benzoic acid standard (Phillipson, 1964). Caloric content of oven dried laboratory chow ranging in weight from 11.58 to 21.18 mg was 4,360 $\pm$ 17.3 cal/g ($N = 28$) and of dried straw samples ranging in weight from 6.67 to 13.25 mg was 4,213 $\pm$ 54.6 cal/g ($N = 21$). Based upon percent composition of the diets, caloric values of the high, medium, and low quality diets were 4,360, 4,323 and 4,287 cal/g, respectively. Because straw is poorly digested (National Research Council, 1971), the differences in available caloric contents

of the diets were much greater than indicated by total caloric content alone.

Upon completion of the experiment, mice were fed laboratory chow for two weeks and were sacrificed on day 35. Tissues were collected for starch gel electrophoresis. Techniques of electrophoresis were essentially those of Selander et al. (1971), Clayton and Tretiak (1972), Harris and Hopkinson (1976) and Breshears et al. (1988). Buffer-stain-tissue-locus combinations can be obtained from the authors. The inheritance of the loci used in this study has not been checked in *P. polionotus* directly, but inheritance inferred from banding patterns is probably correct because of studies of mother-offspring phenotypic combinations in this species (Foltz, 1979), linkage analyses in closely related *Peromyscus* spp. (Dawson, 1982) and inheritance studies in closely related rodents of the same family (listed in Smith et al., 1984). All but one of the 38 variable loci analyzed in the present study are referred to in these general references and/or their quaternary structure is known allowing predictions for the banding patterns of phenotypes of mice heterozygous for a particular locus.

Of the 58 loci examined for each individual, 38 were polymorphic with an average number of 4.9 heterozygous loci per individual. A Mantel analysis of heterozygosity differences and geographic distances of captures detected no significant relationship ($P < 0.95$). Furthermore, utilizing the X^2 test, only one polymorphic locus deviated significantly, albeit marginally ($P = 0.049$), from Hardy-Weinberg equilibrium. Mice were assigned to one of three allozyme heterozygosity classes for data analyses. Mice with three or fewer variable loci were considered to be in the low heterozygosity class ($N = 10$); mice with seven to nine variable loci were in the high class ($N = 9$); the remainder with four to six variable loci were in the middle class ($N = 20$). Because heterozygosity levels were determined after the dietary tests, an unequal number of individuals were included within each heterozygosity class.

Before the caloric content of the feces was determined, feces from the individuals in the high and low heterozygosity classes were combined within each class and dried, weighed, and ground using a mortar and pestle to obtain a uniform powder. Feces from individuals in the middle heterozygosity class were not analyzed because of time constraints. From each blend 12 samples ranging in weights from 7.54 to 15.95 mg were drawn and cal/g of the samples were determined. Differences between the high and low heterozygosity classes were analyzed with a Student's t test.

Dependent variables analyzed using covariance analyses were body weight, weight of food eaten, weight of food absorbed, and efficiency of absorption (weight of food absorbed/weight of food eaten). Efficiency of absorption was also calculated in terms of calories. The experiment was a combination of both nested and repeated measures designs. Initial body weight, as recorded at the start of each dietary treatment was used as a covariate along with the classification variable, heterozygosity class, to analyze the data from that treatment. It was anticipated that initial body weight would be an important factor in an animal's ability to maintain weight during the experiment. Large mice need more food than do small mice, and if increased weight is due to stored energy, can probably lose more weight without exhibiting stress. All analyses were conducted using the SAS system (SAS Institute, 1985). Statistical significance was indicated when $P \leq 0.05$, and highly significant differences were indicated when $P \leq 0.001$. Estimates of variation around means are given as one standard error.

Results

Body weight for all mice decreased when dietary quality decreased (Fig. 1). Mean initial body weight was 13.4 ± 0.236 g and reached its lowest value, 11.8 ± 0.171 g, at the conclusion of the low quality dietary treatment. Declining weight was used as an indicator of stress. Variation in weight was analyzed using an analysis of covariance procedure to determine if an animal's ability to maintain body weight was related to its heterozygosity. Based upon three body weights recorded for each individual within each dietary treatment, least square means were computed for mice in each heterozygosity class (Fig. 2a). When fed diets of high quality, mice within the low and middle het-

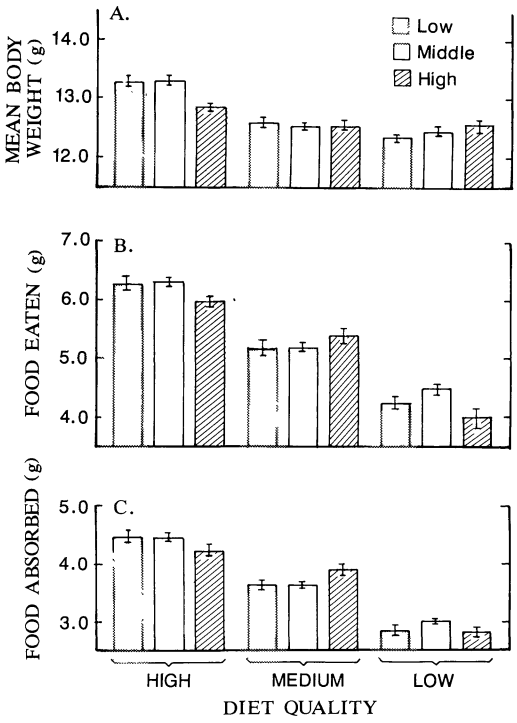

FIG. 2. Least square means for body weight (A), food eaten (B), and food absorbed (C) for mice during each dietary treatment: high, medium, and low. The heterozygosity classes (low, middle, and high) are indicated in the upper right corner. The bars above and below each value represent one standard error.

TABLE 1. Variation in body weight can be attributed to a series of variables and their interactions. The initial body weight (IWT) recorded at the start of each dietary treatment was used as a covariate with heterozygosity class. Treatment (Trmt) refers to three dietary levels. Heterozygosity Class (Htcls) is high, middle, or low allozyme heterozygosity rankings. Each animal was weighed three times for each dietary treatment, after an acclimation period, midway through a measurement period and at the end. Time refers to the time before and after the midpoint. Interaction components are indicated by asterisks and those factors nested within others are bracketed. The error variance was used for *F*-tests except where noted in footnotes.

Source	*df*	SS[4]	*F* Value[5]	*P*
Treatment	2	1.94	1.96[2]	ns[1]
Heterozygosity Class	2	1.81	1.83[2]	ns
Trmt•Htcls	4	1.98	3.41[3]	0.05
Time [Trmt]	6	6.61	7.60[3]	0.001
Time [Trmt• Htcls]	12	1.74	0.48	ns
Initial Weight	1	261.94	870.33	0.0001
IWT•Trmt	2	0.86	1.44	ns
IWT•Htcls	2	1.90	3.15	0.05
IWT•Trmt• Htcls	4	2.23	1.85	ns
Error	315	94.81		

[1] ns equals $P > 0.05$.
[2] Trmt•Htcls used as error term.
[3] Time [Trmt•Htcls] used as error term.
[4] Type III Sums of Squares used.
[5] R^2 equals 0.88.

erozygosity classes tended to be heavier than those in the high heterozygosity class. However, mice that were more heterozygous maintained their weight better than their less heterozygous counterparts when fed lower quality food. By the end of the low quality dietary treatment, the mean weight of those in the high heterozygosity class was greater than that of the mice in the other two classes.

Initial body weight at the beginning of each dietary treatment was a highly significant source of variation (Table 1). The interaction for initial weight and heterozygosity class was significant, further indicating that initial differences in body weight are the primary reason that individuals differed; both heterozygosity and initial weight affected the maintenance of body weight. There was also a significant interaction between dietary treatment and heterozygosity class, which was consistent with the trend that weights of mice in the three heterozygosity classes were affected differently by the treatments (Fig. 2a).

Mice ate a greater volume but lesser weight of food as dietary quality decreased due to the relatively light weight of the straw. Weight of food absorbed was significantly correlated to the weight eaten. Figures 2b and 2c illustrate least square means for food eaten and food absorbed, respectively, for mice within each heterozygosity class. Patterns in weight of food eaten and absorbed were difficult to discern among heterozygosity classes, because the weight of food eaten was affected by body weight (Robbins, 1983). Body weights changed differently during the experiment for mice in each heterozygosity class. Results of the analyses of covariance for food eaten and absorbed were similar (Table 2). In the former the main effect of heterozygosity was significant whereas in the latter it was marginally significant. The interaction between dietary treatment and heterozygosity class was not

TABLE 2. Variation in weight of food eaten, weight of food absorbed and efficiency of absorption (g of food absorbed/g of food eaten) are attributed to a series of sources and their interactions in analyses of covariance. The initial body weight (IWT) recorded at the start of each dietary treatment was used as a covariate in a model that also considered Heterozygosity Class (Htcls). Each sample of food and feces was weighed twice to estimate weighing errors and this source of variation is represented by Sample. Rep is analogous to Time in Table 1 because food and feces were collected twice (at the midpoint of the measurement period and at the end of each dietary treatment). Interaction components are indicated by asterisks, and those factors nested within others are bracketed. The error variance was used for F-tests except where noted in footnotes.

		Food eaten			Food absorbed			Efficiency		
Source	*df*	SS[5]	*F*[6]	*P*	SS[5]	*F*[7]	*P*	SS[5]	*F*[8]	*P*
Treatment[2]	2	1.25	5.14	ns[1]	0.85	2.86	ns	0.001	0.32	ns
Heterozygosity Class[3]	2	10.56	27.87	0.01	2.05	5.26	0.076	0.032	3.02	ns
Sample[4]	1	0.00	0.19	ns	0.00	0.08	ns	0.000	0.09	ns
Rep [Trmt][4]	3	10.92	405.38	0.0001	10.22	297.93	0.0001	0.028	142.26	0.0001
Sample [Trmt•Rep]	5	0.04	0.02	ns	0.06	0.07	ns	0.000	0.06	ns
Trmt•Htcls	4	0.76	0.48	ns	0.78	1.16	ns	0.021	4.74	0.001
Initial Weight	1	18.72	47.75	0.0001	7.02	41.70	0.0001	0.004	3.90	0.05
IWT•Trmt	2	4.74	6.05	0.01	3.20	9.51	0.0001	0.003	1.20	ns
IWT•Htcls	2	10.42	13.29	0.0001	1.92	5.70	0.01	0.034	15.44	0.0001
IWT•Trmt•Htcls	4	1.00	0.64	ns	1.02	1.51	ns	0.023	5.15	0.001
Error	441	172.89			74.24			0.490		

[1] ns equals $P > 0.05$.
[2] A linear combination of Sample [Trmt•Rep] and Trmt•Htcls used as error term.
[3] Trmt•Htcls used as error term.
[4] Sample [Trmt•Rep] used as error term.
[5] Type III Sums of Squares used.
[6] R^2 equals 0.72.
[7] R^2 equals 0.77.
[8] R^2 equals 0.30.

significant. The lack of significance was probably due to the influence of initial body weight on the weight of food eaten and absorbed and to the relatively small sample size. The effects of initial body weight and its interaction with heterozygosity class were both significant.

An examination of efficiency of absorption is more instructive than the analysis of either weight of food eaten or absorbed, because it combines both variables (Fig. 3; Table 2). During the high quality dietary treatment mice had essentially the same average efficiency, about 71%. When fed medium quality diets, the mice with low and middle levels of heterozygosity dropped in efficiency, whereas mice within the high heterozygosity class increased their efficiency. Mice with low and middle heterozygosity levels had their lowest efficiency, 67.3%, when fed low quality diets. Mice with high heterozygosity had almost the same efficiency with the low quality diet (70.9%) as with the high quality diet. Analysis of covariance for feeding efficiency demonstrated a highly significant interaction between dietary treatments and heterozygosity class. The effects of initial body weight and its interaction with heterozygosity class were significant.

Caloric value, as well as quantity of food eaten or absorbed, is important. Caloric values of feces ranged from 3,950 ± 73.1 cal/g for mice with low heterozygosities fed a low quality diet to 3,737 ± 77.3 cal/g for those with high heterozygosities fed a high quality diet. No significant differences were observed when caloric content of the feces from mice in the high and the low heterozygosity classes were compared for each dietary treatment.

Efficiency of absorption can be expressed in grams or calories and the values differ slightly. Percent efficiency based on calories for mice with low and high heterozygosities were identical (75.1%) when fed high quality diets. When fed medium quality diets, the efficiency of the mice with low heterozygosities dropped to 72.1%, while the efficiency of those with high heterozygosities remained the same. During the low quality dietary treatment, the efficiency of mice with

low heterozygosities fell to 69.6%, whereas that of those with high heterozygosities dropped to only 73.5%. Mice with low heterozygosities were not able to absorb calories from food as readily as mice which had high heterozygosities. This difference was most evident under dietary stress.

Differences in efficiencies of absorption and maintenance metabolism were likely causes for the varying abilities of mice to maintain their body weights under dietary stress. Body weights responded quickly to changes in food quality in the laboratory. When mice were fed 100% laboratory chow after the low quality dietary test, their weights increased (Fig. 1).

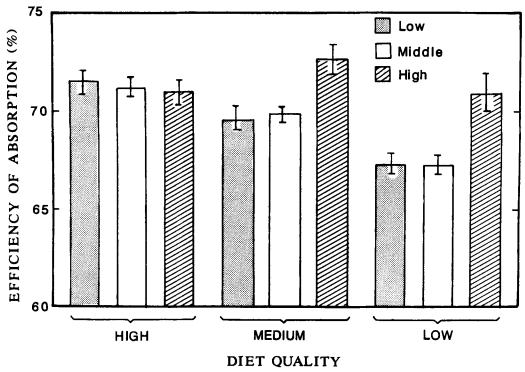

FIG. 3. Efficiency of absorption (weight of food absorbed/weight of food eaten) expressed in percentages for mice during each dietary treatment: high, medium, and low. The heterozygosity classes (low, middle, and high) are indicated in the upper right corner. The bars above and below each value represent one standard error.

DISCUSSION

The amount of food ingested and absorbed determines the amount of energy available for other processes. The energy absorbed is used for maintenance metabolism and secondary productivity. The latter includes growth, energy storage, and reproduction, which are important characteristics that influence fitness. Changes in secondary productivity can result from reallocation of various components of the energy budget. The variables underlying secondary productivity interact, and therefore the potential exists for different reaction norms depending on the state of these variables. Our experiment was designed to measure directly ingestion and absorption and indirectly maintenance metabolism as inferred from changes in body weight. Differences in heterozygosity could be associated with changes in these components as well as changes in the proportion of energy partitioned into growth, storage, and reproduction.

A number of studies have documented correlations between heterozygosity and variables related to secondary productivity. Garton (1984) found a positive relationship between growth rates and heterozygosity in *Thais haemastoma* (a muricid gastropod); growth rates varied significantly because of greater feeding rates for individuals with higher heterozygosities versus those with lower values. Garton et al. (1984) also demonstrated a similar positive relationship for *Mulinia lateralis* (coot clam), which was due to a reduction in maintenance metabolism in clams with higher heterozygosities. Rodhouse and Gaffney (1984) studied *Crassostrea virginica* (American oyster) and concluded that high heterozygotic animals conserve weight better than those of lower heterozygosity under temperature and nutritive stress and that this ability enhances growth. Mitton et al. (1986) found that heterozygosity was negatively correlated with maintenance metabolism but was positively correlated with metabolic rates of active *Ambystoma* (tiger salamander). Protein turnover rates are lower in more heterozygous clams (Hawkins et al., 1986), thus providing a mechanism for reduced maintenance metabolism, growth, and reproductive correlates. Components of the energy budget seem to be correlated, because the total amount of energy to be partitioned is limited. Heterozygosity effects may result from a change in any one of the components. Thus, more heterozygous individuals would have a greater scope for activity (Mitton and Grant, 1984) than individuals that are less heterozygous. This increased scope could result in higher foraging rates and different ingestion rates for individuals of varying levels of genetic variability.

Differences in an animal's metabolic and feeding efficiency, such as those documented in our study (Fig. 3), should have an impact on secondary productivity. Although growth rate has not been correlated

with heterozygosity for *P. polionotus,* that relationship has been reported for other species including *Odocoileus virginianus* (white-tailed deer) (Cothran et al., 1983), *A. tigrinum* (tiger salamander) (Pierce and Mitton, 1982), and *Mytilus edulis* (blue mussel) (Koehn and Gaffney, 1984). Fat stores also vary as a function of heterozygosity in *O. virginianus* (Cothran et al., 1987; Scribner et al., in press). Adult body weight varies as a function of heterozygosity in both *P. polionotus* (Garten, 1976) and *O. virginianus* (Cothran et al., 1983; Scribner et al., in press).

Body weight is a strong correlate of fitness in *P. polionotus.* Large individuals are socially dominant, more successful in intraspecific competition, have an increased propensity for exploratory behavior, and higher reproductive output than small individuals (Garten, 1976, 1977; Kaufman and Kaufman, 1987). Our data indicate that factors determining body weight interact in complex ways (Table 1, Fig. 2a). Body weight of mice was not positively associated with heterozygosity when mice were fed high quality diets, but there was a positive relationship when they were stressed by the low quality diet. Mice with high heterozygosity levels maintained their body weights under dietary stress better than those with low heterozygosity. The ability to efficiently use food for growth is important in determining the fitness of free living mice during unfavorable times when food declines in quality and abundance.

The ability to vary characteristics of secondary productivity under different environmental conditions is extremely important in maximizing fitness. Animals with higher heterozygosity may have greater flexibility in dealing with environmental conditions than those with lower levels (Mitton and Grant, 1984), although this may not always be the case (Brown, 1982). Our data on efficiency of absorption and maintenance of body weight further support this conclusion (Table 2, Fig. 3). Genetically more variable individuals function better in poor environments and about the same in the best environment as their less variable counterparts. Body weight is important in determining the response to different environmental conditions, and it interacts with heterozygosity (Tables 1 and 2). The most heterozygous mice may have more options for achieving maximum fitness by modifying their life history characteristics.

Small changes in certain components of the energy budget, such as efficiency of absorption, can result in large changes in secondary productivity. Since secondary productivity represents less than 2% of the absorbed energy in *P. polionotus* (Odum et al., 1962), changing maintenance metabolism by 1% could result in a 50% change in secondary productivity. Differences in percent efficiency of absorption between animals with high and low heterozygosities fed medium and low quality diets varied as much as 3.0% and 3.9%, respectively. With differences of this magnitude, other components of secondary productivity should vary positively with heterozygosity as has been observed for reproduction in *P. polionotus* (Smith et al., 1975). Changing the efficiency of absorption can have a large effect on certain life history traits that affect other characteristics, such as population density (Smith et al., 1975). There is a need to understand heterozygosity effects in terms of various mechanisms of population regulation and evolution.

Our study supports the prediction of Mitton and Grant (1984) that the relationship between heterozygosity and fitness correlated characters should be more distinct during times of stress than during optimal conditions. The effects of heterozygosity are more obvious with poor quality diets and disappear or are obscured with high quality diets. These data may explain why some studies have failed to demonstrate a relationship between heterozygosity and characters associated with fitness. Testing for correlates of heterozygosity under optimal conditions may fail to show important genetic effects and reveal the evolutionary mechanisms by which heterozygosity alters individual fitness. More studies that utilize an experimental approach are needed to further elucidate the relationship between heterozygosity and fitness.

Acknowledgments

We thank P. L. Leberg and G. D. Hartman for their help in collecting mice. J. Coleman graciously drafted all figures. F.

Allendorf, R. Anderson, R. Chesser, and J. Mitton criticized an earlier version of this manuscript. Research and manuscript preparation were supported by Contract DE-AC09-76SR00-819 between the U.S. Department of Energy and the University of Georgia's Institute of Ecology. W. R. Teska received support for travel by contract S-1944 from Oak Ridge Associated Universities.

Literature Cited

Breshears, D. D., M. H. Smith, E. G. Cothran, and P. E. Johns. 1988. Genetic variability in white-tailed deer. Heredity 60:139–146.

Brown, K. L. 1982. Demographic and genetic characteristics of dispersal in the mosquitofish, *Gambusia affinis* (Family Poeciliidae). Ph.D. Diss. Univ. of Georgia, Athens.

Clayton, J. W., and D. N. Tretiak. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Bd. Canada 29:1169–1172.

Cothran, E. G., R. K. Chesser, M. H. Smith, and P. E. Johns. 1983. Influences of genetic variability and maternal factors on fetal growth in white-tailed deer. Evolution 37:282–291.

———. 1987. Fat levels in female white-tailed deer during the breeding season and pregnancy. J. Mammal. 68:111–118.

Dawson, W. D. 1982. Protein polymorphisms in American deermice (*Peromyscus*) and genetic linkage homology. Acta Theriol. 27:213–230.

Foltz, D. W. 1979. Genetics and mating system of the oldfield mouse (*Peromyscus polionotus*). Ph.D. Diss. Univ. of Michigan, Ann Arbor.

Garten, C. T., Jr. 1976. Relationships between aggressive behavior and genic heterozygosity in the oldfield mouse, *Peromyscus polionotus.* Evolution 30:59–72.

———. 1977. Relationships between exploratory behavior and genic heterozygosity in the oldfield mouse. Anim. Behav. 25:328–332.

Garton, D. W. 1984. Relationship between multiple locus heterozygosity and physiological energetics of growth in the estuarine gastropod *Thais haemastoma.* Physiol. Zool. 57:530–543.

Garton, D. W., R. K. Koehn, and T. M. Scott. 1984. Multiple-locus heterozygosity and the physiological energetics of growth in the coot clam, *Mulinia lateralis,* from a natural population. Genetics 108:445–455.

Harris, H., and D. A. Hopkinson. 1976. Handbook of Enzyme Electrophoresis in Human Genetics. North Holland Publ. Co., Amsterdam.

Hawkins, A. J. S., B. L. Bayne, and A. J. Day. 1986. Protein turnover, physiological energetics and heterozygosity in the blue mussel, *Mytilus edulis*: The basis of variable age-specific growth. Proc. Roy. Soc. Lond. B 229:161–176.

Kaufman, D. W., and G. A. Kaufman. 1987. Reproduction by *Peromyscus polionotus*: Number, size, and survival of offspring. J. Mammal. 68:275–280.

Koehn, R. K., and P. M. Gaffney. 1984. Genetic heterozygosity and growth rate in *Mytilus edulis.* Mar. Biol. 82:1–7.

Mitton, J. B., and M. C. Grant. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. Ann. Rev. Ecol. Syst. 15: 479–499.

Mitton, J. B., C. Carey, and T. D. Kocher. 1986. The relation of enzyme heterozygosity to standard and active oxygen consumption and body size of tiger salamanders, *Ambystoma tigrinum.* Physiol. Zool. 59:574–582.

National Research Council. 1971. Atlas of Nutritional Data on U.S. and Canadian Feeds. National Academy of Science, Wash., DC.

Odum, E. P., C. E. Connell, and L. B. Davenport. 1962. Population energy flow of three primary consumer components of oldfield ecosystems. Ecology 43:88–96.

Palmer, A. R., and C. Strobeck. 1986. Fluctuating asymmetry: Measurement, analysis, patterns. Ann. Rev. Ecol. Syst. 17:391–421.

Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. Oikos 15:130–139.

Pierce, B. A., and J. B. Mitton. 1982. Allozyme heterozygosity and growth in the tiger salamander, *Ambystoma tigrinum.* J. Hered. 73:250–253.

Robbins, C. T. 1983. Wildlife Feeding and Nutrition. Academic Press, N.Y.

Rodhouse, P. G., and P. M. Gaffney. 1984. Effect of heterozygosity on metabolism during starvation in the American oyster *Crassostrea virginica.* Mar. Biol. 80:179–187.

SAS Institute. 1985. SAS User's Guide: Statistics, Version 5 Edition. SAS Institute Inc., N.C.

Scribner, K. T., M. H. Smith, and P. E. Johns. Environmental and genetic effects on growth of white-tailed deer antlers. J. Mammal. *In press.*

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus.* I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics. VI. Univ. Texas Publ. 7103:49–90.

Smith, M. H., C. T. Garten, Jr., and P. R. Ramsey. 1975. Genic heterozygosity and population dynamics in small mammals, pp. 85–102. *In* C. L. Markert (ed.), Isozymes IV. Genetics and Evolution. Academic Press, N.Y.

Smith, M. W., W. R. Teska, and M. H. Smith. 1984. Food as a limiting factor and selective agent for genic heterozygosity in the cotton mouse *Peromyscus gossypinus.* Amer. Midl. Nat. 112:110–118.

Zouros, E., and D. W. Foltz. 1987. The use of allelic isozyme variation for the study of heterosis, pp. 1–59. *In* M. C. Rattazzi, J. G. Scandalios, and G. S. Whitt (eds.), Isozymes: Current Topics in Biological and Medical Research, Vol. 13. Liss, N.Y.

Corresponding Editor: F. W. Allendorf