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Author(s): David W. Foltz, John L. Hoogland and Gary M. Koscielnny

Source: *Journal of Mammalogy*, Vol. 69, No. 3 (Aug., 1988), pp. 611-614

Published by: American Society of Mammalogists

Stable URL: <http://www.jstor.org/stable/1381355>

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EFFECTS OF SEX, LITTER SIZE, AND HETEROZYGOSITY ON
JUVENILE WEIGHT IN BLACK-TAILED PRAIRIE DOGS
(*CYNOMYS LUDOVICIANUS*)

DAVID W. FOLTZ, JOHN L. HOOGLAND, AND GARY M. KOSCIELNY

Department of Zoology and Physiology, Louisiana State University, Baton Rouge, LA 70803

Appalachian Environmental Laboratory, University of Maryland, Frostburg, MD 21532

Department of Biology, Princeton University, Princeton, NJ 08544

Heterozygosity at electrophoretically detected allozyme loci appears to be correlated with fitness components such as growth, fecundity, and viability in organisms representing diverse taxa (Mitton and Grant, 1984; Zouros and Foltz, 1987). Such correlations may have important implications for understanding the maintenance of allozyme polymorphisms in natural populations. Several theories have been proposed to account for the existence of correlations between heterozygosity and fitness components; these have been reviewed by Mitton and Grant (1984) and Zouros and Foltz (1987). For mammals, there have been several reports of heterozygosity-fitness correlations for domestic species, but natural mammalian populations have received less attention in this regard. One potential complication in studying effects of heterozygosity in mammals is that growth and viability of juveniles depend partly on maternal phenotype. For example, in a recent study of white-tailed deer (*Odocoileus virginianus*), Cothran et al. (1983) found that fetal growth was correlated significantly with both fetal and maternal heterozygosity at four allozyme loci. Also, juvenile weight in mammals is often determined partly by litter size (Koepl and Hoffmann, 1981; Phillips, 1981; Turner et al., 1976), and sexual dimorphism in weight is common (Armitage et al., 1976; Dolman and Michener, 1983). The present study was conducted to determine if juvenile weight was associated with litter size, sex, and juvenile or maternal heterozygosity in the black-tailed prairie dog (*Cynomys ludovicianus*). Several reports on genetic variation (Chesser, 1983; Foltz and Hoogland, 1983) have been published recently for *C. ludovicianus*, but the effect of heterozygosity on juvenile weight has not been investigated previously in this species.

Black-tailed prairie dogs are diurnal, colonial rodents living in dry upland prairies. Starting in 1976, behavioral observations were made each spring on individually marked prairie dogs in a colony in Wind Cave National Park, South Dakota (Hoogland, 1985, 1986). In the study colony, copulations generally occurred in February and March, and offspring first appeared above ground in May and June. The average gestation period was 34.8 ± 0.1 ($\bar{X} \pm SE$) days (range, 34-37), based on 32 litters. The average time between parturition and emergence of offspring was 43.4 ± 0.8 days (range, 38-50), as determined from 17 litters (Hoogland, 1985). Each juvenile was trapped soon (usually 3-5 days) after its first emergence. Sex and weight (to the nearest 1 g) were determined, and each animal was ear-tagged for future identification. Each year (except 1986), the study colony also was censused in October, at which time most (96.2%) juveniles still resident in the colony were trapped and weighed. Beginning in 1978, blood samples were taken from approximately 1,200 prairie dogs in the study colony (>95% of the total population) for determination of plasma and red-cell-protein variation. Of 26 loci examined electrophoretically, five were polymorphic: transferrin (*Trf*), esterase-1 (*Est-1*), nucleoside phosphorylase (*Np*), 6-phosphogluconate dehydrogenase (*6-Pgd*), and phosphoglucomutase-2 (*Pgm-2*). However, esterase-1 phenotypes have not been determined since 1981. Phosphoglucomutase-2 (not included in the original survey of electrophoretic variation by Foltz and Hoogland, 1983) has been examined since 1980 and is polymorphic for four alleles. In this paper, maternal heterozygosity refers to the number (from 0 to 4) of loci (of *Trf*, *Np*, *6-Pgd*, and *Pgm-2*) at which the mother of a juvenile is a heterozygote, and juvenile heterozygosity is the corresponding number for the juvenile itself.

The present study is based on animals born between 1980 and 1986. By restricting the analysis to the last 7 years of the study, it was possible to include the highly polymorphic *Pgm-2* locus. During the 7-year period, 653 offspring representing 208 litters were trapped following emergence from the natal burrow. However, electrophoretic data were available at all four loci for both mother and offspring only for 615 offspring and 198 litters. Of the 615 offspring, 287 were female and 328 were male, not significantly different from a 1:1 ratio ($P > 0.05$, G-test). The 198 litters included in the study were produced by 124 mothers, an average of 1.60 ± 0.06 litters per female (range, 1-4). The average number of offspring produced per

TABLE 1.—Effects of various factors on weight at emergence and weight increment in October for juvenile black-tailed prairie dogs (*Cynomys ludovicianus*). Degrees of freedom (d.f.), type I sums of squares (SS), and F values are shown.

Source of variation	At emergence			In October		
	d.f.	SS	F	d.f.	SS	F
Litter size (LS)	5	2.369	4.98***	5	0.089	0.22
Maternal heterozygosity (MH)	4	0.418	1.10	4	0.248	0.76
LS × MH	16	2.295	1.51	15	0.968	0.79
Error (among litters within LS × MH)	172	16.367		111	9.077	
Sex of offspring (SO)	1	0.237	80.66***	1	0.148	7.09**
Offspring heterozygosity (OH)	4	0.012	1.00	4	0.055	0.66
OH × SO	4	0.004	0.30	4	0.011	0.13
OH × SO × LS	29	0.098	1.14	27	0.453	0.80
MH × OH × SO	32	0.124	1.31	24	0.302	0.60
MH × OH × LS	22	0.086	1.33	11	0.088	0.38
MH × SO × LS	12	0.023	0.65	4	0.040	0.48
MH × OH × SO × LS	10	0.037	1.26	3	0.067	1.07
Error (residual)	303	0.891		92	1.927	

** P < 0.001.
*** P < 0.0001.

female during the study period was 4.96 ± 0.24 (range, 1–13). These values do not represent average lifetime reproductive output per female, because they exclude litters born before 1980 or after 1986. The average litter size at emergence was 3.11 ± 0.08 (range, 1–6). The average maternal heterozygosity was 2.05 ± 0.08 (range, 0–4). Of the 483 recently emerged offspring trapped between 1980 and 1985, 318 (65.8%) were present in the study colony in the following October (but only 306 were weighed at that time) and 278 (57.6%) were present the following spring. During the 1st year of life, most disappearances occurred in summer rather than in winter. More importantly for the present paper, the 318 animals present in October averaged heavier at emergence (151.4 ± 1.6 g) than the 165 animals that disappeared (139.1 ± 2.3 g). Also, the 278 animals present at 1 year of age averaged heavier than the 205 that disappeared, in terms of both weight at emergence (151.7 ± 1.7 g as opposed to 141.2 ± 2.1 g) and weight in October (546.2 ± 4.9 g as opposed to 508.8 ± 18.5 g). Assuming that most disappearances were a result of mortality, weight was correlated positively with viability, a more direct component of fitness.

The analysis was performed using the general linear models procedure in the Statistical Analysis System (SAS Institute Inc., 1985). The two dependent variables were juvenile weight at first emergence and weight increment in October (weight in October minus weight at first emergence). The weight data were log_e-transformed before analysis to ensure homogeneity of variances. Although the main emphasis of the study was on genetic effects, as represented by observed heterozygosity at four allozyme loci, it also was necessary to consider other factors potentially affecting juvenile weights. In some species of ground-dwelling squirrels, juvenile growth rates (either prenatal or postnatal) may be affected by litter size or sex. Of the four main effects of interest, two (maternal heterozygosity and litter size) were treated as maternal effects and two (offspring heterozygosity and sex) as individual effects. Thus, the statistical model was a split-plot design (Cochran and Cox, 1957; Sokal and Rohlf, 1981), with the 198 litters treated as “plots” and the individual offspring considered “subplots.” The main difference between this design and a conventional four-factorial analysis of variance is that the appropriate error mean square for testing effects at the plot level is the variance among litters within litter size-maternal heterozygosity classes. The remaining effects (those representing offspring heterozygosity and sex, either as main effects or as interactions with other main effects) were tested appropriately for significance over the conventional residual error mean square.

Male offspring were significantly heavier than female offspring (Table 1), both at emergence (150.9 ± 1.5 g, $n = 328$ as opposed to 145.8 ± 1.6 g, $n = 287$) and in October (553.3 ± 7.2 g, $n = 159$ as opposed to 528.3 ± 6.6 g, $n = 147$). Litter size was a statistically significant source of variation in juvenile weight at emergence (Table 1); mean weight at emergence decreased with increasing litter size, at least to a litter size of five (Table 2). Other investigators of ground-dwelling squirrels have found similar results (Koepl and Hoffmann, 1981; Phillips, 1981; Turner et al., 1976). However, there were no significant differences among litter-size classes in weight increment in October (Tables 1 and 2), suggesting that the effect of litter size on juvenile weight does not persist much past weaning. Neither maternal heterozygosity nor offspring heterozygosity were significant sources of variation in juvenile weight, and none of the interaction terms was

TABLE 2.—Mean juvenile weight (in g) at emergence and mean growth increment (in g) in October, with samples sizes (n) and standard errors, for different litter sizes in black-tailed prairie dogs (*Cynomys ludovicianus*).

Litter size	At emergence		In October	
	n	$\bar{X} \pm SE$	n	$\bar{X} \pm SE$
1	16	201.1 \pm 11.2	11	389.3 \pm 29.0
2	84	154.2 \pm 3.2	51	395.7 \pm 10.3
3	198	152.6 \pm 2.0	124	390.7 \pm 6.7
4	224	143.3 \pm 1.4	84	391.1 \pm 10.0
5	75	136.4 \pm 3.0	27	373.1 \pm 12.6
6	18	145.7 \pm 5.2	9	404.3 \pm 11.6

significant. Consideration of sums of squares in Table 1 revealed that most variation in juvenile weights (71% at emergence, 67% in October) was attributable to variation among litters within litter-size and maternal-heterozygosity classes. This variation could be related to variation among litters in gestation period, lactation period, or interval between weaning and emergence; variation among years in food availability; nutritional or other phenotypic differences among females within years; or effects of loci other than those included in the electrophoretic survey. The pattern in which the whole-plot error is larger than the subplot error is common in split-plot designs (Cochran and Cox, 1957). In biological terms, the consequence of this large amount of among-litter variation is a reduced ability to detect effects acting at the level of entire litters. Zouros and Foltz (1987) noted that the greater the control over environmental sources of variation in a phenotypic trait, the more likely it is that a significant correlation will be detected between the trait and allozyme heterozygosity. Therefore, the present results do not provide strong evidence for or against the hypothesis that maternal heterozygosity has an effect on juvenile weight. There was a (statistically nonsignificant) trend for mean weight at emergence to increase with increasing maternal heterozygosity, but no such trend was evident for weight increment in October. In contrast to the situation for maternal effects, the large among-litter variation should have no effect on ability to detect the effect of individual heterozygosity on juvenile weight, so the conclusion that offspring heterozygosity was not associated with juvenile weight probably is robust. The most important unresolved question of the present study is the source of the large among-litter variation in juvenile weight. Determining the cause or causes of this variation requires additional research.

We thank the 105 assistants who have helped with the field work, and we especially thank T. Anderson, P. Hardison, J. Hoogland, M. Hoogland, S. Hoogland, P. McDonald, S. Partan, and P. Walsh. We also thank the staff at Wind Cave National Park, especially R. Klukas, L. McClanahan, and E. Ortega. Laboratory help was provided by J. Gee, L. Whitcomb, B. Glidewell, and L. Hanson, and statistical advice was provided by Dr. J. Geaghan, Dr. A. Saxton, and P. Culley. We thank Dr. G. R. Michener and two anonymous reviewers for comments on an earlier version of the manuscript. Hoogland acknowledges support by National Science Foundation grants BNS 77-15594, BNS 79-24093, DEB 81-02791, and BSR 83-07705, National Geographic Society grants 78-1860, 79-2063, and 84-2776, the American Philosophical Society, the Center for Field Research, the Eppley Foundation for Research, the Max McGraw Wildlife Foundation, the Whitehall Foundation, the Harry Frank Guggenheim Foundation and the Universities of Maryland, Michigan, and Minnesota. Foltz acknowledges support by National Science Foundation grant BSR 84-07450. This is contribution number 1795-AEL from the Appalachian Environmental Laboratory, the University of Maryland's Center for Environmental and Estuarine Studies.

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Submitted 13 October 1986. Accepted 18 June 1987.

J. Mamm., 69(3):614–618, 1988

CHANGES IN KIDNEY MASS IN THE INDIAN MONGOOSE (*HERPESTES AUROPUNCTATUS*)

BRUCE E. COBLENTZ AND DIRK VAN VUREN

Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331 (BEC)
Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045 (DVV)

Kidney mass-body allometry has been established among adult terrestrial mammals (Brody, 1945; Prothero, 1984); Prothero (1984) reported that kidney mass in adult terrestrial mammals varied as the 0.85 ± 0.01 power of body mass. Such a precise relationship, however, does not account for the nonproportional kidney mass-body mass relationship across the entire range of body size of a species; juvenile feral sheep have been shown to have proportionally larger kidneys than adults (Van Vuren and Coblentz, 1985). Additionally, kidney mass varies seasonally within some species and not necessarily as a function of body mass (Anderson, 1981; Batcheler and Clarke, 1970; Dauphine, 1975; Mitchell et al., 1976; Pucek, 1970; Van Vuren and Coblentz, 1985). The cause of variation in kidney mass is uncertain. Mammalian kidneys have several functions, including regulation of water balance and excretion of metabolic wastes (Romer, 1970), and these organs produce substantial quantities of heat (Chaffee and Roberts, 1971). Suggested causes of variation in kidney mass fall into three general categories that reflect kidney physiology: body-water kinetics (Dauphine, 1975; Pucek, 1970; Van Vuren and Coblentz, 1985), somatic metabolic activity (Batcheler and Clarke, 1970; Flux, 1971), and temperature stress (Chaffee and Roberts, 1971).

The objectives of this study were to determine if kidney mass changes seasonally in the Indian mongoose (*Herpestes auropunctatus*) in Virgin Islands National Park and to relate changes in kidney mass to seasonal aspects of the life history of the species or its environment. The mongoose was chosen for study because in the U.S. Virgin Islands it is an exotic, destructive, and undesirable mammal trapped in large numbers as part of a program to protect eggs and hatchlings of nesting hawksbill turtles (*Eretmochelys imbricata*), an endangered species (Coblentz and Coblentz, 1985a).

The island of St. John (18°20'N, 64°44'W) was described briefly by Coblentz and Coblentz (1985b). Mongooses ($n = 1,009$) were trapped from January through November 1983 in 15 by 15 by 45 cm live traps (National Live Trap Co., Tomahawk, WI) baited with 50–60 g of fresh fish or fish heads. Traps were set in 20 low-elevation locations and reset in 12 of these at least once (Coblentz and Coblentz, 1985a).

Mongooses were transported to the laboratory each day, sacrificed, and weighed. Sex and age (juvenile or adult) were recorded for all animals, and reproductive activity (pregnancy and lactation) was recorded