# DENSITY-DEPENDENT EFFECTS ON GROWTH, BODY SIZE, AND CLUTCH SIZE IN BLACK BRANT

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ABSTRACT.—We documented gosling size in late summer, adult body size, and clutch size of known-age Black Brant (*Branta bernicla nigricans*) females nesting on the Tutakoke River colony between 1986 and 1995. During this period, the colony increased from 1,100 to >5,000 nesting pairs. Gosling mass at 30 days of age declined from 764 ± SE of 13 g and 723 ± 15 g for males and females, respectively, in the 1986 cohort, to 665 ± 18 g and 579 ± 18 g in the 1994 cohort. Gosling size was directly negatively correlated with number of Black Brant broods. We detected no trend in adult body size for individuals from these cohorts; in fact, adults from the 1992 and 1994 cohorts had the largest overall masses. Clutch size increased with age from 3.4 eggs for 2-year-old females to 4.4 eggs for 5-year-old females. Clutch size declined during the study by 0.20 (3-year-old females) to 0.45 (2-year-old females) eggs. Clutch size did not decline between the 1986 and 1990 cohorts for females that were >5 years old. Our results for clutch size and gosling size are similar to those recorded for Lesser Snow Geese (*Chen caerulescens caerulescens*). Our failure to detect a trend in adult body size, however, differs from the response of other geese to increasing population density. We interpret this difference in effects of density on adult size between Black Brant and other geese as an indication of stronger selection against the smallest individuals in Black Brant relative to other species of geese. *Received 19 May 1997, accepted 17 November 1997.*

ARCTIC-NESTING GEESE are strictly herbivorous during the breeding season (Owen 1980, Sedinger 1992) and are selective of the most nutritious foods and habitats containing these foods (Lieff 1973, Harwood 1975, Sedinger and Raveling 1984, Gadallah and Jefferies 1995a, b). Despite these strong preferences, substantial variation exists in growth rates of goslings, which likely is associated with temporal and spatial variation in habitat quality (Cooch et al. 1991a, Larsson and Forslund 1991, Sedinger and Flint 1991, Aubin et al. 1993). Because gosling growth is associated with future survival and fecundity (Larsson and Forslund 1991, 1992, Francis et al. 1992, Rockwell et al. 1993, Sedinger et al. 1995b), habitat quality likely is directly linked to processes determining population dynamics. Sedinger and Raveling (1986) argued that seasonal declines in nutrient

concentration in the diet of Cackling Canada Geese (*B. canadensis minima*) resulted from reduced availability of the highest-quality foods because of grazing by geese. Lesser Snow Geese (*Chen caerulescens caerulescens*) substantially reduce the abundance of preferred food plants (Cargill and Jefferies 1984, Hik and Jefferies 1990), as do some Black Brant (*B. bernicla nigricans*; hereafter brant; Person et al. 1998).

The relationship between nutrient intake by goslings and demographic parameters creates the potential for per capita availability of foods of sufficient quality during brood rearing to influence population dynamics. Long-term declines in body size and fecundity have been associated with increased size of a colony of Lesser Snow Geese, and Cooch et al. (1991a, b) and Francis et al. (1992) demonstrated a decline in juvenile survival for this colony over the same period.

The number of brant nesting on the Yukon-Kuskokwim (Y-K) Delta declined by more than 60% in the 1970s and early 1980s (Sedinger et al. 1993), likely as a result of human harvest (Sedinger 1996) and predation by arctic foxes (*Alopex lagopus*; Anthony et al. 1991, Sedinger et al. 1993). Reduced predation and harvest were as-

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sociated with a more than four-fold increase in the Tutakoke River colony between 1985 and 1992 (Sedinger et al. 1993, Anthony et al. 1995). Increase in colony size created the opportunity to examine changes in demographic parameters as the population increased. Because the initial decline most likely was a result of factors independent of food supply, the dynamics of the population represent a large-scale removal experiment. Herein, we examine changes in gosling growth, adult body size, and clutch size over the period of increase for brant breeding at the Tutakoke River colony.

## METHODS

This study was conducted on the Tutakoke River brant colony (61°N, 165°W) and associated brood-rearing areas on the outer coastal fringe of the Y-K Delta, Alaska. Brant have been studied continuously at this site since 1984 and sporadically since the 1950s (Sedinger et al. 1993). The area is characterized by low saltmarsh vegetation interspersed with tidal sloughs and areas of bare mud (Kincheloe and Stehn 1991). Brant nest in meadows within 1 km of the Bering Sea coast, and they rear their broods up to 30 km from the colony. Adults lead their broods to relatively small (<2 km²) home ranges within about a week of hatching (Flint unpubl. data). We captured brant on brood-rearing areas during the molting period of adults by herding them into corral traps when goslings were from about 24 to 38 days old ($\bar{x}$ = 30 days). Each individual received a U.S. Fish and Wildlife Service metal band and a 2.5-cm-high plastic band engraved with three alphanumeric characters. Individuals originally banded as goslings provided a known-age sample when observed in subsequent years, whereas individuals originally banded as adults provided a sample whose minimum age was known because they were ≥2 years old when banded. We weighed a sample of previously banded adults (±10 g) and goslings (±5 g) in each banding drive. All goslings that had been web-tagged in the nest (see below) were weighed and measured. We also measured culmen and tarsus length on the same individuals using dial calipers (±0.1 mm). We measured diagonal tarsus, which includes the end of the tarsometatarsus bone (Dzubin and Cooch 1992).

When approximately 10% of pairs had initiated nests, we began searching about 50 ($\bar{x}$ = 49, range 40 to 52) 50-m radius plots that were randomly placed throughout the colony. Each plot was searched every four days until egg laying was complete. During late incubation and throughout hatching, we systematically searched the entire colony, attempting to locate all nests associated with at least one color-banded adult. We individually marked all eggs when first

found in nests on plots and in nests of marked adults. Each such nest also was marked with an individual marker located about 1 m from the nest, and nest locations were mapped on 1:10,000 aerial photographs. We attempted to visit all nests of marked adults on their hatching day, at which time no. 1 fish fingerling tags were placed in the webs of all goslings that were hatched or in pipped eggs (Alliston 1975). Web-tagging provided a sample of known-age goslings when we captured them later in the summer.

We calculated a Lincoln-Peterson index (Poole 1974) using the number of marked adult females observed during nesting as the initial marked sample to assess the trend in the number of nesting pairs using the brood-rearing areas we sampled. We then used the number of marked and unmarked females captured during banding drives to calculate an index of the number of pairs using brood-rearing areas. These calculations provide only an index of number of pairs because we were unable, for logistic reasons, to sample all brood-rearing areas. Use of a Lincoln-Peterson index assumes that the population is closed (no deaths, emigrations, or immigrations) between release and recapture of marked individuals (Poole 1974). Some adults lose their nests (Sedinger unpubl. data), or their broods and leave the area (Flint et al. 1995), between recording their bands and potential recapture during banding. Emigration will not bias Lincoln-Peterson estimates unless marked individuals emigrate differentially (Seber 1973). Furthermore, we have not observed trends among years in nesting (Sedinger unpubl. data) or brood success (Flint et al. 1995) that might have caused a trend in bias in Lincoln-Peterson indices.

All analyses using linear models were performed using the General Linear Models (GLM) procedure of SAS (SAS 1989). We analyzed variation in gosling mass and culmen and tarsus lengths among cohorts using a model in which sex was a main effect, and age in days and cohort were covariates. Because we did not web-tag goslings in 1986, we estimated age of goslings (in days) at capture as the number of days between peak hatching date and date of capture. We were justified in modeling growth as a linear function of age in days because growth of goslings is approximately linear over the range of ages we encountered (24 to 38 days; Cooch et al. 1991a, Sedinger et al. 1995b). To directly examine the relationship between gosling size and brood number, we also performed an analysis in which mean gosling mass for males and females in each cohort (adjusted for age at capture) was the dependent variable, sex was a fixed factor, and number of broods was the covariate.

We were interested primarily in long-term trends in growth, adult body size, and clutch size. Nevertheless, shorter-term annual fluctuations in the number of broods might be associated with annual vari-
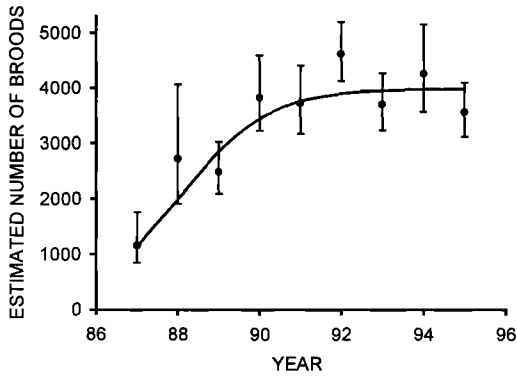
FIG. 1. Lincoln-Peterson estimates of number of Black Brant broods using brood-rearing areas on which goslings and adults from the Tutakoke River colony were measured. Fitted curve is the logistic function $N(t) = A/(1 + \exp[b + kt])$, where $A = 3,394$, $b = 0.925$, and $k = 0.920$. Parameters estimated using PROC NONLIN (SAS 1989).

ation in growth rate. Furthermore, the relationship between brood density and growth could be nonlinear because of a lag between effects of grazing and food abundance. We have observed an increase in foraging habitat because grazing changes the morphology of an abundant sedge to a short form preferred by brant. Therefore, we expected that deviation from the trend in brant numbers would be associated with a deviation from the trend in gosling growth. For example, the presence of fewer broods than expected during the population increase might result in a temporary increase in food abundance, because grazing habitat was created the year before, thereby increasing per capita food abundance. To examine the relationship between annual variation in brood density and variation in growth rate, we first fit a logistic function to our indices of numbers of broods (PROC NONLIN; SAS 1989). We then calculated residuals from the fitted trend for each year. We used a model with sex as a fixed effect to examine the relationship between residuals from the long-term trend in gosling mass and residuals from the logistic fit to the trend in brood numbers.

We examined variation among cohorts in adult body size by randomly selecting one set of measurements of mass, culmen, and tarsus for each color-banded individual, initially marked as a gosling, captured at ≥1 year old. We analyzed variation in each of these measurements using a model with cohort, sex, and calendar year as main effects in the model because of the potential for masses to vary among years, independent of cohort (Eichholz 1996). We also examined trends in adult measurements across cohorts using linear regression of measurements on cohort. To analyze variation in clutch size, we randomly selected one record for each marked known-age female in the sample. We then used a two-factor (cohort and age) model to analyze variation among both ages and cohorts. In each GLM, we followed the approach of modeling effects of variables and two-way interaction among variables. We then removed nonsignificant interactions from models. All hypothesis tests were based on Type III sums of squares.

## RESULTS

The number of families using brood-rearing areas we sampled increased from 1,162 in 1987 to 4,612 in 1992, after which numbers fluctuated (Fig. 1). We measured 1,362 known-age goslings in this study. Male goslings were heavier than female goslings (Table 1), and body mass of goslings declined by 16% across cohorts (Table 1, Fig. 2) after we adjusted for age at capture. Similar patterns existed for culmen and tarsus lengths (Table 1, Fig. 2), although these skeletal structures declined less than mass (5% and 3.5%, respectively). The adjusted mean mass of goslings declined with increasing number of broods ($F = 12.9$, df = 1 and 18, $P = 0.003$). Residuals from the long-term trend in gosling mass (Fig. 2) were negatively related to residuals from the logistic trend in brood numbers ($F = 11.7$, df = 1 and 13, $P = 0.0046$; Fig. 3); goslings were smaller

TABLE 1. General linear model results of analysis of variance in mass, culmen, and tarsus of Black Brant goslings with respect to cohort, sex, and age in days. Calculations of mean square (MS) based on Type III sum of squares.

| Source | Mass | | | | Culmen | | | | Tarsus | | | |
|--------|------|------------|-----|---------|------|---------|-----|---------|------|---------|-----|---------|
|        | df   | MS         | F   | P       | df   | MS      | F   | P       | df   | MS      | F   | P       |
| Cohort | 1    | 4,754,843  | 393 | <0.0001 | 1    | 62,993  | 192 | <0.0001 | 1    | 252,394 | 204 | <0.0001 |
| Sex    | 1    | 697,210    | 58  | <0.0001 | 1    | 8,280   | 25  | <0.0001 | 1    | 215,352 | 174 | <0.0001 |
| Age    | 1    | 10,701,480 | 884 | <0.0001 | 1    | 258,802 | 790 | <0.0001 | 1    | 719,827 | 581 | <0.0001 |
| Error  | 1,359| 12,102     |     |         | 1,352| 327     |     |         | 1,351| 1,239   |     |         |

FIG. 3.   Relationship between residuals from the trend in Black Brant gosling mass (Fig. 2) and residuals from the trend in numbers of broods (Fig. 1).
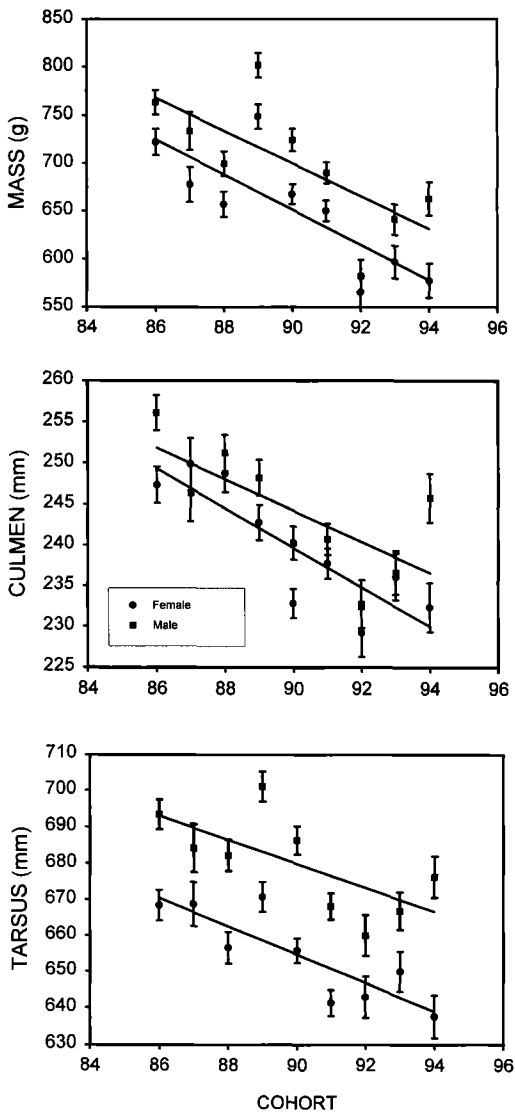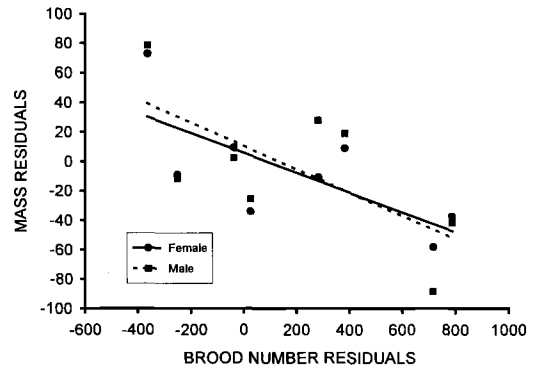
FIG. 2.   Trends in mass and culmen and tarsus lengths (±SE) of Black Brant goslings from the 1986 through 1994 cohorts. Measurements adjusted for age (days) in the summer of capture.

than expected in years when more broods than expected were present.

Adult body mass varied between the sexes ($F = 11.81$, df = 1 and 149, $P = 0.0008$) and among years ($F = 3.42$, df = 7 and 149, $P = 0.002$) and tended to vary among cohorts ($F = 1.83$, df = 8 and 149, $P = 0.075$). There was no trend in adult mass across cohorts ($F = 0.1$, df = 1 and 156, $P = 0.71$). Adult tarsus length differed between the sexes ($F = 7.65$, df = 1 and 150, $P =$

0.006) and among cohorts ($F = 2.82$, df = 8 and 150, $P = 0.006$) and tended to vary among years ($F = 2.06$, df = 7 and 150, $P = 0.051$). As for mass, there was no trend in adult tarsus length across cohorts ($F = 3.01$, df = 1 and 157, $P = 0.08$). Adult culmen length did not vary significantly between the sexes ($F = 2.54$, df = 1 and 150, $P = 0.11$), among years ($F = 0.28$; df = 1 and 150, $P = 0.96$), or among cohorts ($F = 1.00$, df = 8 and 150, $P = 0.44$).

Clutch size varied among age classes of females and among cohorts (Table 2). Clutch size declined across cohorts for known-age females, although visual inspection of Figure 4 suggests that clutch size did not decline for 5-year-old females. Clutch size did not decline for females >5 years old for whom we knew only minimum age ($F = 2.50$, df = 1 and 179, $P = 0.12$); the slope of the relationship between clutch size and year was actually positive for >5-year-old females.

## DISCUSSION

*Growth and body size.*—The decline in gosling size as colony size increased is consistent with patterns in Lesser Snow Geese (Cooch et al.

TABLE 2.   General linear model results for variation in clutch size of Black Brant among age classes (years) and cohorts.

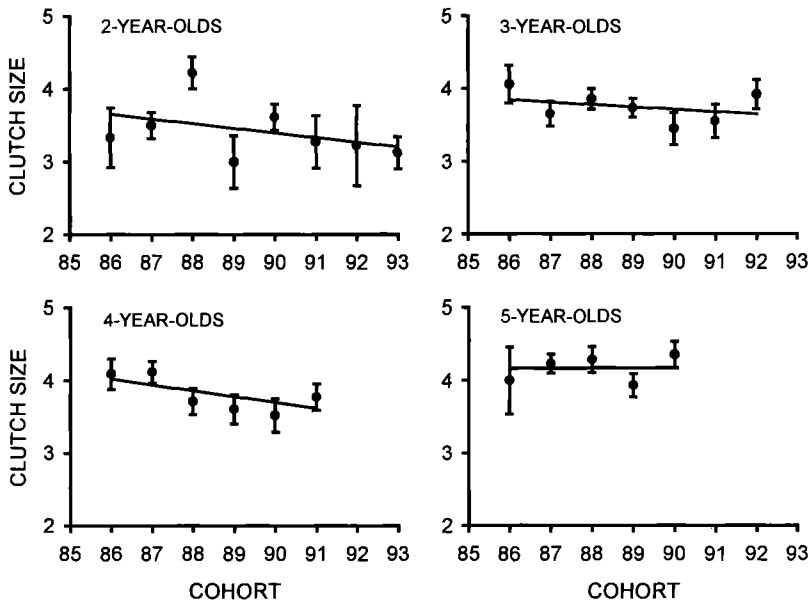| Source | df | MS | F | P |
|---|---|---|---|---|
| Age | 3 | 8.01 | 8.3 | <0.0001 |
| Cohort | 1 | 4.47 | 4.6 | 0.032 |
| Error | 549 | 0.98 | | |

FIG. 4.   Clutch sizes of known-age female Black Brant from the 1986 to 1993 cohorts.

1991a). Slower growth in response to higher population density most likely is related to reduced food abundance. Brant increased the amount of time devoted to feeding as population density increased (Sedinger et al. 1995a), consistent with the response to a higher density of broods in Cackling Canada Geese (Sedinger and Raveling 1988, Fowler and Ely 1997). Slower growth probably does not represent a genetic response by the brant population for several reasons. First, there is little evidence for an important genetic role in variation in growth in the population we studied (Sedinger and Flint 1991, Sedinger et al. 1997a). Cooch et al. (1991a) also found that slower growth of Lesser Snow Geese primarily was of environmental origin. Larsson and Forslund (1992) found significant heritability of body size in Barnacle Geese (*Branta leucopsis*), but common environment and maternal effects undoubtedly inflated their heritability estimates relative to the additive genetic contribution to the trait in question. Second, selection is strong against slowly growing goslings in the Tutakoke River population (Sedinger et al. 1995b). Finally, the decline in growth rate that we report occurred over less than two generations. We believe that it is unlikely that the complex suite of physiological and metabolic traits associated with a genetically determined target

growth rate (Tomas et al. 1988, Marks 1993a, b) could change substantially over so short a period.

Metrics of adults varied among cohorts despite no trends across cohorts in adult size. We are unsure of the mechanism underlying this variation, but it could reflect variation among years in size-based selection on goslings (e.g. Sedinger et al. 1995b) or variation in postfledging growth conditions. Body mass of adults also varied among years, after controlling for cohort of origin, which likely reflected annual variation in pre- or postnesting foraging conditions for adults.

*Dynamics of gosling growth and colony size.—* The number of nesting pairs increased six-fold between 1985 and 1991, after which colony size fluctuated (Sedinger et al. 1993, Anthony et al. 1995). We cannot explain short-term fluctuations in number of broods using brood-rearing areas, but we note that two of the largest deviations from the population trajectory (Fig. 1) occurred in years (1989 and 1992) when nesting was delayed by late snow melt (Lindberg et al. 1997). Interestingly, in one of these years (1989), fewer broods were present than expected based on the trajectory of the population increase, whereas in the other year (1992), more broods were present than expected. We suspect that these short-term fluctuations reflect some

combination of availability of nest sites, age structure of the potential breeding population, and food abundance on spring staging areas (Lindberg et al. 1997). Especially important was that growth of goslings was associated with the number of broods using brood-rearing areas; goslings grew faster in 1989 than in any other year of the study, and they grew most slowly in 1992 when we estimated the largest number of broods on the brood-rearing areas. Overall, deviations in gosling body mass from the long-term decline were negatively correlated with deviations from the long-term trend in the number of broods.

Rapid growth of goslings in 1989 requires explanation because the number of broods in 1989 was comparable to that in 1988 and greater than that in 1987 (and likely 1986). We hypothesize that rapid growth of goslings in 1989 resulted from a nonlinear relationship between food availability and population size. Virtually no broods used brood-rearing areas in 1984 and 1985, because predation by arctic foxes destroyed more than 95% of the nests on the colony (Anthony et al. 1991). *Carex subspathacea* "grazing lawns" maintained by geese (Jefferies 1989) increase in biomass substantially in the absence of grazing by geese (Bazely and Jefferies 1986, Person et al. 1998), and brant avoid grazing such vegetation (Sedinger pers. obs.). We observed an increase in the aerial coverage of *Carex* grazing lawns during the 1990s in response to increased grazing by larger numbers of geese breeding on the Y-K Delta in the 1990s. Therefore, we hypothesize that geese have increased the aerial coverage of grazing lawns during the period of population increase, but that increases in the area of grazing lawns have lagged behind the population increase. Clearly, the hypothesized increase in area of grazing lawns has not been sufficient to fully compensate for the increased population size, hence the density-dependent decline in growth rate observed over the period of the study. The maximum possible aerial coverage of grazing lawns must reflect a balance among grazing pressure by the geese themselves, the response of vegetation to grazing, and physical factors, such as soil salinity. The area of grazing lawns may have been higher in 1989 than in 1988, explaining the rapid growth of goslings in 1989, when the number of nesting pairs was temporarily reduced.

*Life-history consequences of slower growth.*— Slower-growing goslings within cohorts survived their first year at a lower rate than goslings that grew more rapidly (Sedinger et al. 1995b). We have also observed a decline in first-year survival of brant as population size has increased (Sedinger et al. 1997b), similar to the pattern observed in Lesser Snow Geese (Francis et al. 1992). In Lesser Snow Geese, adult size and clutch size declined as population size increased (Cooch et al. 1991b). In contrast, we did not detect a decline in adult body size in brant associated with the decline in growth rate, although gosling size is correlated with adult size in brant (Sedinger et al. 1995b). The absence of a decline in adult size in brant, therefore, suggests selection against an increasing proportion of cohorts as mean size of goslings declined. Lower first-year survival of goslings from more recent cohorts is consistent with such changes in selection. It is not clear, however, why adult body size could decline in Lesser Snow Geese but not in brant, in response to slower gosling growth. We hypothesize that brant are near the minimum viable size for obligate avian herbivores given their life-history characteristics, which reduces the potential for adult body size to respond to poor foraging conditions during growth.

We observed a decline in clutch size across cohorts among females ≤4 years old, but not among older females. This trend in clutch size among younger females cannot be explained by a decline in adult body size, because adult size did not decline. We hypothesize that smaller clutch size in younger females from later cohorts resulted from the declining ability of these females to compete for food during prenesting, when nutrient reserves that contribute to breeding (Ankney 1984) are stored. If successful competition is dependent on social status, which likely is affected by age, then younger, but not older, females would have smaller nutrient reserves and, consequently, smaller clutches as population size increased.

This study and others (Cooch et al. 1991a, b, Francis et al. 1992) demonstrate important density-dependent effects on processes that influence population dynamics. These findings have important implications for management. We also believe that the dynamic interactions among food, growth, life-history traits, and fitness provide an important opportunity to bet-

ter understand fitness of particular genotypes and reaction norms to environmental variation (Stearns 1992).

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*Associate Editor: T. E. Martin*