Altitudinal Variation in Body Size and Population Density of *Nicrophorus investigator* (Coleoptera: Silphidae)

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ABSTRACT Increasing altitude may influence insect communities, population sizes, life-histories, and morphology. *Nicrophorus investigator* Zetterstedt, a holarctic species, occurs over a range of elevations in the western Rocky Mountains of North America. This study examines changes in population density, seasonal activity periods, morphology, and reproduction at three sites over an elevational gradient in the southern Rocky Mountains of Colorado. *N. investigator* population sizes varied yearly at both low (≈2,800 m) and high (≈3,200 m) elevations, but were always greater at the lower elevations. Adult activity at all sites began in late June, remained relatively constant throughout July, and declined by late August. Elytron length was highly correlated both with body mass and pronotum width. There was no difference in elytron length between males and females (within years, sites). However, elytron length was significantly greater in 5 out of 6 yr at the higher elevation site, and in 1999, at two additional low and high elevation sites in separate drainages. Beetles at the low and high elevation sites differed slightly in their reproductive strategies under captive conditions. At the high elevation, the number of larvae did not increase with carcass size, thus larvae from larger carcasses weighed more than larvae reared on smaller carcasses. At the low elevation, brood size tended to increase with carcass mass, resulting in similar-sized larvae across all carcass masses. On average, brood growth efficiency (total brood grams/carcass grams) was higher at the higher elevation, perhaps explained by developing at lower temperature. These results indicate that both life-history strategies and developmental processes may be involved in the elevational variation seen in this species.

KEY WORDS *Nicrophorus*, body size, elevation, larval development, population dynamics, reproduction

ELEVATION HAS DRAMATIC effects on species composition and population density in dung beetle (Hanski and Cambefort 1991), copro-necrophagic beetle (Martin-Piera and Lobo 1993), and butterfly (Gutierrez and Menendez 1995) communities. Increasing altitude tends to mimic latitudinal gradients, with more variable and extreme climatic conditions leading to decreased resources, population sizes, and diversity. Additionally, elevation can influence life-history strategies, particularly those related to reproduction, larval growth, and development. Because elevational changes are often considered to simulate a range of climates, studies of life-history strategies at different elevations have been applied to estimate the effects of climate warming (Sparks et al. 1995).

Studies of altitudinal variation in life-history patterns in insects (Baldwin and Dingle 1986, Janzen et al. 1976, Coxwell and Bock 1995, Sparks et al. 1995, Sota 1996, Blanckenhorn 1997, Tatar et al. 1997) have linked life-history variation to soils or climate, particularly temperature, as well as to changes in competitors and resource availability (Sota 1996, Smith and Merrick 2000). Extensive theoretical work on the evolutionary tradeoff between offspring size and number predicts that more competitive environments or shorter seasons (such as may occur at higher elevations) will favor fewer, larger offspring (Parker and Begon 1986, Lloyd 1987).

Body size also changes across latitudinal and altitudinal gradients. However, in insect species, size does not vary regularly with elevation. Some species are larger at higher elevations (Stalker and Carson 1948, Miller 1991, Hawkins and Devries 1996, Krasnov et al. 1996), some smaller (Janes 1994, Hawkins and Devries 1996, Sota 1996, Blanckenhorn 1997, Krasnov et al. 1996), and some show no change at all (Hawkins and Devries 1996, Krasnov et al. 1996). Interest in this pattern, particularly the link between elevation, developmental temperature, and body size has recently been fueled by the debate on the adaptive nature of Bergmann size clines in ectotherms (Van Voorhies 1996, 1997; Mousseau 1997; Partridge and Coyne 1997). Studies measuring body size, life-history characters, development, and population dynamics over a temperature gradient will assist in distinguishing the

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factors responsible for clinal variation among populations.

Nicrophorus investigator is one of three species of burying beetle native to the montane regions of western North America (Peck and Kaulbars 1987, Smith and Heese 1995). Despite the number of studies on *Nicrophorus* reproduction (reviewed in Scott 1998), and the wide area over which many species occur, only one study (Trumbo 1990a) has described latitudinal or altitudinal variation in morphology or reproductive behaviors. Given the strong dependence of *Nicrophorus* reproduction on discrete carcass resources it is likely that life-history strategies as well as morphology may vary with resource availability and type (Holloway and Schnell 1997, Trumbo and Thomas 1998, Smith and Merrick 2000). These types of patterns have been demonstrated in studies of ecologically similar dung beetles (Hanski and Cambefort 1991). Studies of *Nicrophorus* along an elevational gradient have the potential to distinguish between behavioral and physiological responses to temperature and resource gradients.

The purposes of this study were to measure the variation in population size of *N. investigator* across seasons, years, and elevations; to identify morphological differences in *N. investigator* across these temporal and spatial parameters, and to determine whether life-history characters, reproductive strategies, and developmental parameters vary across elevations.

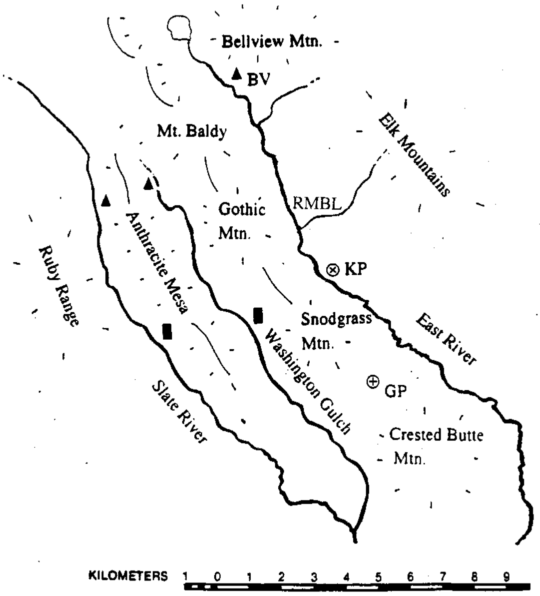

Fig. 1. Seven study sites within three drainages in Gunnison County, CO: Δ BV, Bellview Mountain, 3,170 m; ⊗ KP, Kettle Ponds, 2,866 m; ⊕ GP, Grouse Point, 2,930 m; ▲, upper Washington Gulch, 3,310 m; ▪, lower Washington Gulch, 2,880 m; Δ, upper Slate River 3,185 m; ▪, lower Slate River 2,780 m.

Materials and Methods

Study Organism. Both *N. investigator* and *Nicrophorus defodiens* Mannerheim occur at the study sites (voucher specimens deposited at the Nebraska State Museum). However, *N. defodiens* is much less abundant and less is known about its behavior at this site. *N. investigator* appears to be univoltine (Scott 1998; R.J.S., unpublished data). Adults are diurnal and reproduce throughout the short montane summer. Adults search for carcasses, locating them by scent. A male attracts females to a carcass by means of pheromones (Eggert and Müller 1989). When a female arrives at a carcass she determines its suitability for burial, and (if suitable) begins the process of burial and carcass preparation. Competition for the carcass occurs both as direct interactions with later-arriving beetles and as exploitative interactions (quick burial increases success). Mating occurs during the burial process, as the carcass is prepared in the underground chamber. Eggs are laid soon after and hatch within days. Young larvae require parental feeding; larval growth depends exclusively on the carcass resource located and prepared by both parents. The parents attend the brood and carcass in the underground chamber for 12–18 d. When larvae consume the carcass they move into adjacent chambers where they will overwinter as prepupae. The following summer they pupate and eclose as reproductive adults. In Colorado, *N. investigator* depends on small mammal carcasses for reproduction and prefers warm, open meadows to cooler spruce or aspen forest habitats (Smith and Heese 1995). Carcass selection and burial behaviors, biparental care, and reproductive decisions of *Nicrophorus* in other habitats are well-described (Milne and Milne 1976; Wilson and Fudge 1984; Kozol et al. 1988; Trumbo 1990b, 1990c, 1991, 1996; Sikes 1996; Eggert and Müller 1997; Scott 1998; Miller et al. 1998).

Study Sites. We conducted our study in the vicinity of the Rocky Mountain Biological Laboratory (RMBL), located in the Upper East River Valley, Gothic, Gunnison County, CO (latitude 38° 57′, sp. longitude 107° 00′; 2,900 m elevation). Typically, snow-melt occurs on 23 May (Rocky Mountain Biological Laboratory weather station), ground temperatures reach 10°C around 15 June, and *Nicrophorus* adults emerge in mid- to late June. Initially we chose three study sites (Fig. 1) at two different elevations: (1) Kettle Ponds: an open gently sloping (10°) low elevation (2,866 m) meadow located 2.5 km south of Rocky Mountain Biological Laboratory in Gunnison National Forest, 200–500 m east of the East River. The habitat is characteristic of the fescue community type described by Langenheim (1962), (2) Grouse Point: an open gently sloping, low elevation (2,930 m) meadow located 7 km south of Rocky Mountain Biological Laboratory in Gunnison National Forest, 1,000 m west of the East River, where the vegetation is similar to Kettle Ponds, and (3) Bellview Mountain: an open more steeply sloping (20°) high elevation (3,170 m) meadow located 6 km north of Rocky Mountain Biological Laboratory in Gunnison National Forest, 200–500 m east of the East River. Vegetation was characterized as an upland herb community (Langenheim 1962). The soil was considerably more rocky and less stable than at the Kettle Ponds and Grouse Point sites because of talus accumulation and movement of sediment and debris (Langenheim 1962). Mean annual and mean summer soil temperatures at 50 cm depth were estimated to differ between the high and low elevations sites by ≈0.75–1°C annually and 2–2.5°C during the summer months (Jensen 1984). In 1999 we added four additional sites located in two adjacent drainages: Slate River, low = 2,780 m, high = 3,185 m; Washington Gulch, low = 2,880 m; high = 3,310 m (Fig. 1).

Beetle Abundance and Size. To determine abundance and average sizes of *Nicrophorus* at different elevations, we conducted a biweekly census at the three sites between late June and mid-August for the years 1996–1998, and less frequently in 1994–1995. In 1996–1998 we established one trap line at each site (Kettle Ponds, Grouse Point, and Bellview Mountain) with 10 traps spaced 20 m apart. Traps consisted of metal cans (18 cm deep, 15 cm diameter), pierced to allow drainage, half-filled with soil, and covered with a wire-mesh lid fashioned into a funnel shape and held on with a large rubber band. We suspended each trap ≈40 cm in the air by wiring it to a wooden stake (this reduced vertebrate scavengers and potential injury to livestock from buried traps). We baited the traps with a fresh chicken drumstick 2 d before the beginning of the census period. Traps were checked every day for five consecutive days. Censuses were repeated every other week for 8 wk. All three sites were censused simultaneously.

The census sites and strategies varied in some years. In 1994–1995 we collected beetles using the above methods at Kettle Ponds, and in 1995 we added the Grouse Point site. In 1994 we intensively trapped, measured, and marked beetles at the Bellview Mountain site at carcasses and also in can traps. In 1995 we did not census regularly at Bellview Mountain because there was a very late and heavy snow year. We did, however, collect beetles intermittently in can traps and at carcasses. In 1999 we deleted the Grouse Point site from our censuses, and instead captured beetles at four new sites, paired high and low elevations in the Slate River and Washington Gulch drainages (Fig. 1). At each of these sites we placed three traps 25 m apart and checked them once per week, 12 July through 5 August 1999.

During each census we recorded the number of beetles per trap and the species of *Nicrophorus (N. investigator* or *N. defodiens*) captured. In addition, we sexed each beetle, measured the length of its elytron using digital calipers (Digimatic model CD-6″B, Mitutoyo, Japan) and marked each beetle with 1-mm triangular or square cuts on the end or side of its elytron (Goldwasser et al. 1993). A unique combination of these marks indicated census period and site. We handled and released each beetle at the site of capture. We noted the specific mark upon recapture. We calculated Schnabel population estimates from our mark-recapture data for each site and year (Sutherland 1996). The Schnabel test estimates population sizes from multiple marking and census periods. We calculated mean elytron length for each year, site, and sex, using data from the first capture of each beetle.

To determine the relationship between elytron length and body mass, we transported 117 male and 118 female *N. investigator* to the laboratory, measured and weighed them, and then returned them alive to the site of capture. To determine the relationship between elytron length and pronotal width, 108 *N. investigator* and 102 *N. defodiens* specimens (collected in Colorado and deposited in the Entomology Collection, Nebraska State Museum) were measured to the nearest 0.01 mm with digital calipers. We used a linear regression analysis (Abacus Concepts 1993) to examine the relationship between these body size variables and to allow transformation from one measure to the other.

Beetle Reproduction. To determine if there are differences in reproductive strategies and subsequent reproductive success for *N. investigator* at different elevations, we carried out captive breeding experiments under natural light and temperature conditions at 2,900 m at RMBL and at 3,200 m on Bellview Mountain. For carcasses, we used small mammals that are native to the area (deer mouse, *Peromyscus maniculatus* Wagner; montane vole, *Microtus montanus* Peale; jumping mouse, *Zapus princeps* Allen; least chipmunk, *Tamias minimus* Bachman; pocket gopher, *Thomomys talpoides* Richardson) and are used for reproduction by *N. investigator* (Smith and Merrick 2000).

Captive experiments in 1997–1999 consisted of placing individual freshly thawed carcasses in a metal can filled with dirt (18 cm deep, 15 cm diameter, small holes in bottom to allow drainage, wire mesh lid held on with large rubber band, buried 15 cm into the soil). All of the carcasses were within the weight range accepted by *N. investigator* (Smith and Heese 1995). To each can we added a recently wild-caught (in that location) male and female *N. investigator.* If the adults successfully reproduced, the larvae were removed after they had completed development (usually 14–20 d) and were counted and weighed. We obtained data from 29 broods at the low elevation site (1997–1999) and 20 at the higher elevation (1997–1998). We compared brood size, average larval weight/brood, and total brood weight at the high and low elevation sites using an analysis of covariance (ANCOVA) with site as factor and carcass mass as the covariate regressor (Abacus Concepts 1991). We also examined the relationship between carcass mass and brood size, average larval weight/brood, and total brood mass using regression analysis (Abacus Concepts 1993).

Results

Abundance. *N. investigator* was much more abundant than *N. defodiens* in every year and at all sites. Captures of *N. defodiens* represented <5% of all *Nicrophorus* captures. The following results (except for the correlation between elytra length and pronotum width) refer to *N. investigator.* In addition, there was

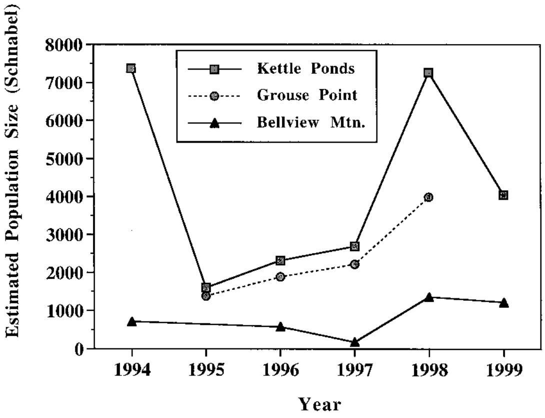

Fig. 2. Estimated population sizes of *N. investigator* at three sites (Kettle Pond and Grouse point, lower elevations; Bellview Mountain, higher elevation).

little movement among sites. Fewer than 30 marked beetles moved between the Kettle Ponds and Grouse Point sites. We did not capture any marked beetles that had moved between the Bellview and Kettle Ponds or Grouse Point sites.

Estimated *N. investigator* adult population size varied among years, but was consistently higher at Kettle Ponds and Grouse Point, the lower elevation sites, than at Bellview Mountain (Fig. 2; combined years 1994, 1996–1999 comparison of Kettle Ponds and Bellview Mountain: $\chi^2 = 765.9$, df = 4, $P < 0.001$). Population size also varied seasonally, with a plateau in late July and early August (Fig. 3). Adult populations declined throughout August and into early September.

Morphology. Elytron length (millimeters) was strongly correlated with body mass (grams) in both sexes (males: $F = 238.2$; df = 1, 90; $P < 0.0001$; $r^2 = 0.728$; regression equation: elytra mm = 6.491 + 8.812 * grams; females: $F = 220.47$; df = 1, 86; $P < 0.0001$; $r^2 = 0.722$; regression equation: elytra mm = 5.952 + 10.434*grams). Elytron length was also strongly correlated with pronotal width (combined sexes) for both *N. investigator* ($F = 375.74$, $n = 108$; $P < 0.0001$; $r^2 = 0.780$) and *N. defodiens* ($F = 1181.64$, $n = 102$, $P < 0.0001$; $r^2 = 0.922$). The mean elytron length of *N. investigator* varied by year, but was significantly greater in 5 out of 6 yr at Bellview Mountain, the higher elevation site (Fig. 4). This pattern was also found at high and low elevation sites in two adjacent drainages (Fig. 5) analysis of variance (ANOVA): $F = 7.943$; df = 1, 322; $P < .005$). There was no significant difference (within any year or site) between the sexes in elytron length (Table 1).

Reproduction. There was no significant effect of year on the reproductive variables so we combined years for analysis. We have also restricted the analysis to the range of carcasses that were successfully used at both high and low elevations (18–38 g). At Bellview, brood size did not increase with increased carcasses mass (ANOVA, $F = 1.150$; df = 1, 18; $P = 0.30$). In contrast, at RMBL, there was a marginally significant increase in brood size with an increase in carcass mass (ANOVA, $F = 3.490$; df = 1, 27; $P = 0.07$). At Bellview, average larval mass increased significantly with carcass mass (ANOVA, $F = 6.852$; df = 1, 18; $P = 0.02$), whereas at RMBL it did not (ANOVA, $F = 1.383$; df = 1, 27; $P = 0.25$). To determine the effect of elevation on average larval mass, brood size and total brood weight while controlling for the varying carcass masses, we employed an ANCOVA, with carcass mass as the regressor and elevation as the factor. There was no significant effect of elevation on total brood mass (Fig. 6; $F = 0.54$; df = 1, 38; $P = 0.47$). The significant effect of site on average larval mass ($F = 6.66$; df = 1, 38; $P = 0.014$) was confounded by a significant interaction effect between site and mouse carcass weight ($F = 5.54$; df = 1, 38; $P = 0.024$). There was a significant elevation effect on brood size ($F = 4.85$; df = 1, 38; $P = 0.033$), with greater brood size at the higher elevation site (Fisher protected least significant difference, $P = 0.002$).

Discussion

We found considerable year-to-year variation in population sizes of *N. investigator* at all of our sites. However, the lower elevation sites supported consistently larger populations of adult beetles, and these populations appeared to fluctuate more dramatically than the higher elevation site. The dynamics of population size may be correlated with small mammal populations. In a parallel study, Smith and Merrick (2000) have found a significant positive correlation between rodent biomass in one year and beetle population size the following year. Estimating *Nicrophorus* populations has always been problematic (Kozol et al. 1988) in part because beetles that are actively reproducing underground are not available for recapture and because we have little information on how far they disperse (Veith 1983, Creighton and Schnell 1998). We chose to employ the Schnabel population estimate because it estimates population sizes based on multiple recaptures across censuses, and would therefore increase the opportunity to recapture beetles over an 8- to 10-wk period. Our main interest was in making relative estimates among sites, not in determining absolute densities. Understanding burying beetle population dynamics is limited by the lack of specific models that address these problems, by low recapture rates, and by the difficulty of measuring resource availability.

That elytron length is positively and strongly correlated with body mass gives us a useful tool for quick field measurements of body size. Elytron measures also correlate with measures of pronotum width, so either measure could be used. We did not find any significant differences in mean adult body size (elytra mm) between males and females for *N. investigator* at any site or in any year. This supports earlier descriptions by Bliss (1949). The lack of size dimorphism suggests similar selective pressures on body size and perhaps a lack of sexual selection on body size. Body

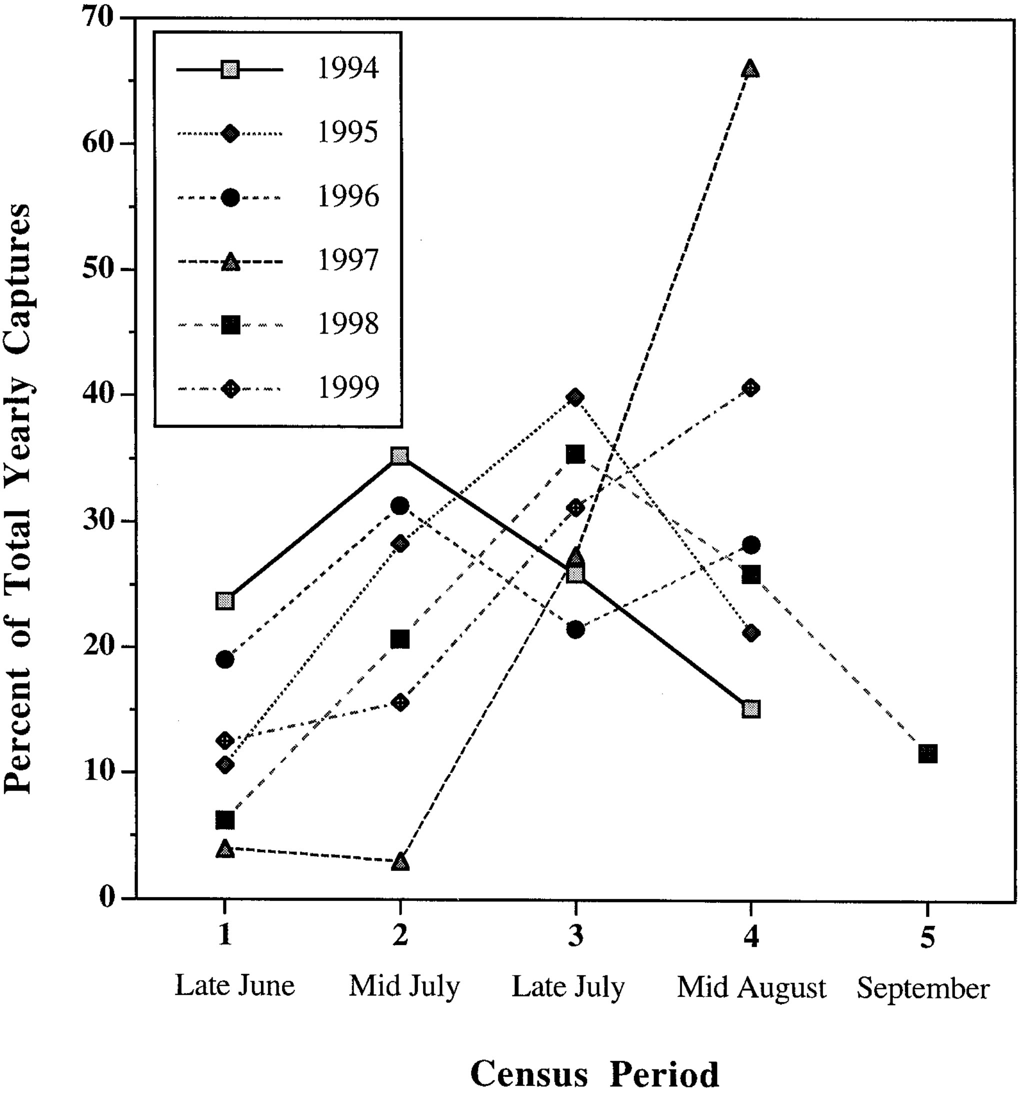

Fig. 3. Percent of total yearly captures during each census period.

size is an important determinant of successful carcass defense and burial, and both sexes engage in intrasexual competition at carcasses (Otronen 1988). Several species of *Nicrophorus* are dimorphic in body size, and it would be intriguing to determine which ecological or behavioral factors influence the evolution of dimorphism within this genus.

In the East River Valley, adult beetles at the higher elevation site were significantly larger than at lower elevations in 5 out of 6 yr. This result is strengthened by additional evidence from independent populations of beetles in the two adjacent drainages, Washington Gulch and Slate River. The pattern of larger body size at higher elevations occurred despite variation in body size over the 6 yr. Trumbo (1990) demonstrated that larger *Nicrophorus* larvae pupate into larger, more successful adults, thus we focused our explanation of adult body size differences on reproductive strategies and larval size.

The brood results indicate that there are different reproductive strategies at the two elevations. In the field, beetles encounter a range of carcass sizes, a feature of their environment that we attempted to mimic in our experiments, although this led to difficulty in interpreting the results. Interestingly, the beetles from the two elevations had slightly different strategies in response to variation in carcass mass. At the high elevation, brood size remained similar (averaging ≈16 larvae) across a twofold range of carcass mass, resulting in larger larvae emerging from the larger carcasses. In contrast, at the lower elevation, brood size was adjusted to match carcass mass (averaging from 8 up to 13 larvae), resulting in similar-sized larvae across the same twofold range in carcass mass.

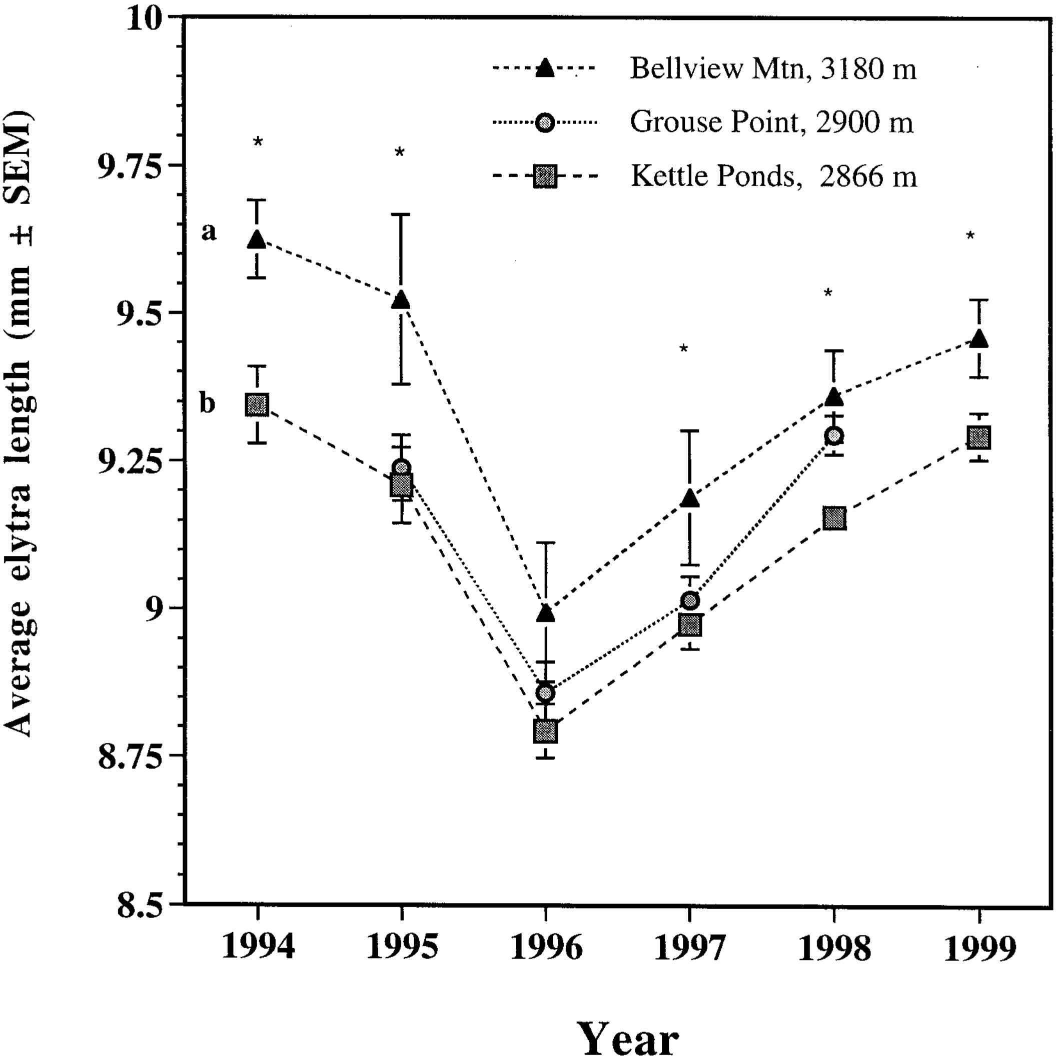

Fig. 4. Mean ± 1 SEM elytron length of *N. investigator* at three sites (Kettle Pond and Grouse Point, lower elevations; Bellview Mountain, higher elevation). a,b, * Indicates significant difference at $P < 0.05$. Sample sizes as follows. Kettle Ponds: 1994, $n = 234$; 1995, $n = 231$; 1996, $n = 472$; 1997, $n = 580$; 1998, $n = 1996$; 1999, $n = 661$. Grouse Point: 1995, $n = 303$; 1996, $n = 341$; 1997, $n = 612$; 1998, $n = 922$. Bellview Mountain: 1994, $n = 234$; 1995, $n = 30$; 1996, $n = 78$; 1997, $n = 84$; 1998, $n = 143$; 1999, $n = 167$.

This second strategy is what is typically described for *Nicrophorus* (Scott 1998) and specifically what we have found previously for *N. investigator* at the lower elevation site (Smith and Heese 1995). It is therefore possible that beetles at the higher elevation are producing larger larvae by selecting larger carcasses on which to breed. Although we have some data on small mammal availability and carcass size at Bellview, we do not yet have information on *Nicrophorus* carcass selection behaviors. We are currently undertaking studies to determine whether the behavioral decisions made by adults (carcass choice and brood size) can explain the significantly larger adult size seen at the higher elevation.

An alternative explanation for larger body size relies directly on the influence of developmental temperature on growth. The result that beetles at the higher elevation were able to raise significantly more larvae at any given carcass mass than those at lower elevation indicates that there are measurable differences in growth efficiencies between the sites. Danks (1994) reviews a variety of life-history studies showing that insects that develop at lower temperatures grow more slowly, have higher assimilation efficiencies, and complete development at a larger size. In addition, fluctuating temperatures during development also tend to increase body size. It is likely that *Nicrophorus* developing at higher elevations are subjected to both cooler

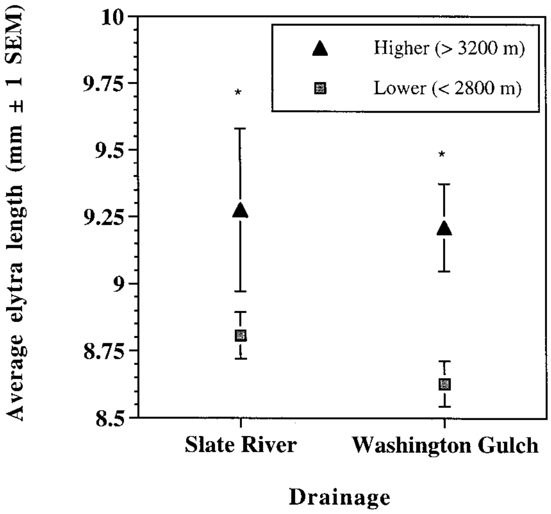

Fig. 5. Mean ± SEM elytron length of *N. investigator* at high and low elevations in two additional drainages (1999). * Indicates a significant difference, $P < 0.05$ (Slate River high elevation, $n = 11$, low elevation, $n = 131$; Washington Gulch high elevation, $n = 31$, low elevation, $n = 153$).

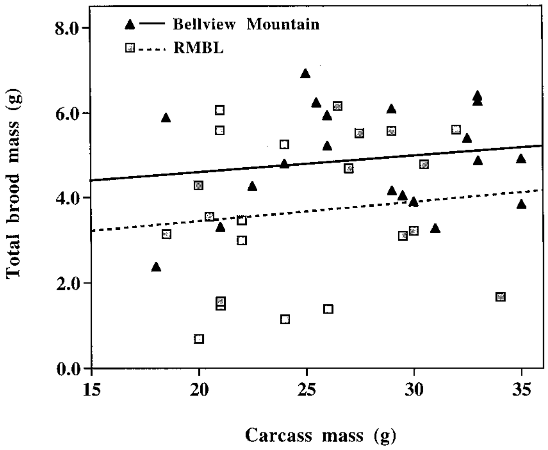

Fig. 6. Growth of broods (total brood mass versus carcass mass) at the lower (Gothic, 2,900 m) and higher elevation sites (Bellview Mountain, 3,250 m), from combined brood data across years.

and more variable ground temperatures. Our results did demonstrate higher growth efficiency at the higher elevation site, but this resulted in larger broods, not larger larvae. Thus, the larval developmental effect, though present, fails to explain the pattern of adult body size we find in our censuses. Bartlett and Ashworth's (1988) evidence that smaller larvae put relatively more mass into final adult body size than larger larvae provides an additional mechanism for increasing body size. Controlled experiments at different temperatures rearing broods all the way through to adulthood would be necessary to determine whether temperature is an important determinant of adult size at emergence.

There are a number of reasons why large body size may be advantageous at higher elevations. Large larvae may have increased overwinter survival (Tepedino and Torchio 1982, Honek 1986). In addition, larger adult beetles are more likely to win when competing for carcasses (Bartlett 1988, Otronen 1988). Large adult beetles may be better at conserving heat, providing them with a thermomuscular advantage when they arrive at carcasses and engage in physical disputes, as was described for dung beetles (Heinrich and Bartholomew 1979). If resources are scarcer at higher elevations, and competition for them is greater, then there may be greater selection for larger body size. Such a selective environment was suggested to explain why *N. defodiens* are larger on islands where they encounter an increased frequency of conspecifics (Trumbo and Thomas 1998).

In conclusion, our studies of *N. investigator* in the Rocky Mountains of Colorado indicate that, despite interannual variation, consistent patterns of size and life-history characters can be found along altitudinal gradients. The change in temperature with elevation is clearly an important component linking the physi-

Table 1. Comparison of mean ± SEM elytron length of male and female *N. investigator*

Site	Year	Male			Female			*t*-test	
		n	Mean	SEM	*n*	Mean	SEM	*t*	*P*
Kettle Ponds	1994	92	9.53	0.093	87	9.40	0.101	0.891	0.38
	1995	123	9.24	0.098	108	9.21	0.086	−0.229	0.82
	1996	251	8.73	0.063	221	8.87	0.066	1.471	0.14
	1997	256	8.94	0.062	323	9.01	0.056	0.863	0.39
	1998	809	9.11	0.037	940	9.20	0.032	1.672	0.09
	1999	299	9.25	0.058	362	9.33	0.052	0.930	0.35
Grouse Point	1995	176	9.26	0.075	126	9.23	0.081	−0.201	0.84
	1996	163	8.82	0.077	147	8.90	0.078	0.801	0.42
	1997	262	8.99	0.063	350	9.03	0.054	0.475	0.64
	1998	372	9.27	0.053	454	9.33	0.047	0.863	0.39
Bellview Mountain	1996	36	8.93	0.178	42	9.05	0.161	0.531	0.60
	1997	38	9.11	0.185	46	9.26	0.139	0.655	0.51
	1998	73	9.22	0.099	63	9.52	0.123	1.869	0.06
	1999	78	9.33	0.094	89	9.58	0.092	1.912	0.06

ology of growth and development to behavior and population dynamics, though it likely interacts with competition and resource density. The results of this and future studies may provide insight into the basic developmental and evolutionary processes that underlie population differentiation as well as serve as an important tool for understanding how the life-history strategies of animal species' may respond to environmental change.

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