

Grasshopper populations across 2000 m of altitude: is there life history adaptation?

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Life history differentiation along climatic gradients may have allowed a species to extend its geographic range. To explore this hypothesis, we compared eleven *Omocestus viridulus* (Orthoptera: Acrididae) populations along an altitudinal gradient from 410 to 2440 m in Switzerland, both in the field and laboratory. In situ temperature records indicated a striking decline in available heat sums along the gradient, and field populations at high altitudes reached egg hatching and adulthood much later in the year than at low elevation. The reproductive period at high altitude is thus severely limited by season length, especially during a cool year. However, controlled environment experiments revealed that intrinsic rates of embryonic and juvenile development increased with the populations' altitude of origin. This countergradient variation is largely genetic and conforms to predictions of life history theory. No corresponding differentiation in the overwintering egg stage, a pivotal determinant of phenology, was found. This trait seems conserved within the gomphocerine grasshopper subfamily. Although we found evidence for altitudinal adaptation in development, the potential of *O. viridulus* to adapt to cool alpine climates appears restricted by a phylogenetic constraint.

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The seasonal recurrence of adverse climatic conditions is a principal force shaping ectotherm life cycles in temperate regions. Growth, development, reproduction and dormancy need to be coordinated and timed in relation to the available growing season (Taylor and Karban 1986, Danks 1994). The set of adaptations, which synchronizes the life cycle with the growing season, is reflected in the organisms' phenology (Tauber et al. 1986). The length of the growing season generally declines with increasing latitude and altitude. Thus, geographically widespread species have to cope with a variety of climatic conditions, which can basically be achieved in two – not mutually exclusive – ways. Firstly, a generalist genotype may display plastic responses in

relation to environmental conditions (Gotthard and Nylin 1995, Schlichting and Pigliucci 1998). Phenotypic plasticity in traits relevant to seasonal timing has been documented and interpreted in adaptive terms in several insect species (Tanaka and Brookes 1983, Nylin 1994, Blanckenhorn 1997, Kingsolver and Huey 1998). Secondly, spatial variation in selection pressures may give rise to genetic differentiation between populations due to natural selection. Prerequisites are heritable genetic variation and restricted gene flow between local populations (Slatkin 1987). Both responses, local adaptation and phenotypic plasticity, may allow a species to extend its distribution across a range of altitudes and latitudes. Several studies of ectotherms report genetic life history

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differentiation in relation to systematic geographic variation in climate (Masaki 1967, Berven and Gill 1983, Dingle et al. 1990, Ayres and Scriber 1994, Blanckenhorn and Fairbairn 1995, Telfer and Hassall 1999, Merilä et al. 2000; but see Lamb et al. 1987). However, almost all studies focus on latitude, whereas evidence for altitudinal life history adaptation in animals is exceedingly scarce. This distinction matters indeed: altitudinal changes in climate typically occur on a particularly small spatial scale, where continuous gene flow is likely to impede genetic differentiation unless strong local selection is acting.

An insect species with a remarkable altitudinal distribution is the grasshopper *Omocestus viridulus* (Acrididae: Gomphocerinae). In Switzerland, it occurs in grasslands from below 400 m to above 2500 m (Thorens and Nadig 1997), making it a suited system for the study of altitudinal adaptation. Over the whole range, it displays an annual life cycle, which includes egg hatch in spring, four larval instars followed by adult molt in summer, and reproduction until autumn. The species overwinters as an egg in embryonic diapause (Ingrisch and Köhler 1998). This dormant phase is characterized by suppressed development, reduced metabolism, and high tolerance to harsh environmental conditions (Danks 1987, Leather et al. 1993). The developmental stage during diapause strongly influences later phenology, as it determines how many developmental steps an embryo has to pass through before hatch in spring. In addition, seasonal timing can be achieved through adjustment of development rates (Danks 1987). Higher rates of embryonic and larval development allow reaching adulthood, and thus the subsequent reproductive phase, sooner. The diapause stage, as well as embryonic and larval development rates, can be identified as chief traits determining phenology, and are therefore of high significance to geographic life history adaptation.

Along the altitudinal gradient, *O. viridulus* faces a decline in the length of the growing season, which is likely to require phenological adjustment. Moreover, the species is sedentary (Ingrisch and Köhler 1998) and most populations are separated to some extent by migration barriers, suggesting rather low levels of gene flow. For these reasons, we hypothesize that local life history adaptation, rather than phenotypic plasticity, allowed the grasshopper to extend its distribution to the wide range of altitudes. In this case, the species would represent a fine-grained patchwork of local demes, which are differentiated in traits relevant to seasonal timing. We address the hypothesis by both field and laboratory approaches. In a first step, the natural temperature regimes and their effect on field phenologies along the gradient are explored. In a second step, we compare populations with respect to developmental rates and diapause characteristics in common laboratory environ-

ments. The latter approach serves to remove environmental variation and reveal genetic differences in life histories, if they occur.

Materials and methods

Study populations

The present investigation includes a total of eleven *Omocestus viridulus* populations. The study sites were chosen to form a transect from the Swiss lowland into the Alps, covering an altitudinal gradient of 2000 m (Fig. 1). Distribution data were provided by the Swiss center of cartography of the fauna (CSCF). We considered only sites where large populations had been reported over several years. Some 110 km separate the furthest sites. Although this spatial scale is relatively small, the study populations can be viewed as reasonably independent, as most populations of this widespread species are isolated to some degree by natural and human dispersal barriers (e.g. forests or farmland).

Field studies

To estimate the length of the growing season in the field, temperatures were recorded hourly during the 2002 season at sites 1, 5, 7 and 10 (see Fig. 1) by means of data loggers ("StowAway TidbiT", Onset Computer Corporation, Bourne, MA, USA). We were primarily interested in the conditions the embryos (eggs) experience. Since *O. viridulus* lays its clutches into the top soil layer or at the base of grass tussocks (Ingrisch 1983, Berner unpubl.), we positioned the loggers' sensors at 1 cm soil depth under natural vegetation cover. Two loggers were used per site, and their measurements averaged for all calculations. Two different indices of

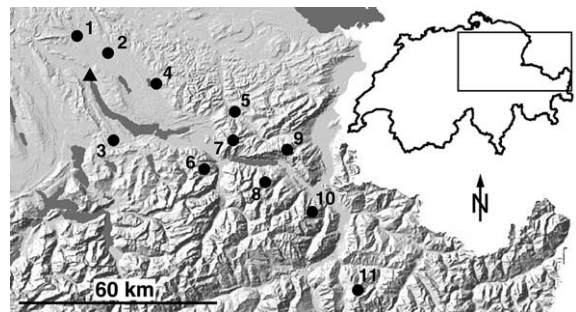


Fig. 1. The rectangle in the outline map shows the location of the study area in Switzerland. The sampling sites and corresponding altitudes are 1) Neerach 410 m, 2) Birchwil 540 m, 3) Schönenberg 670 m, 4) Bäretswil 830 m, 5) Bendel 1055 m, 6) Näfels 1350 m, 7) Speer 1610 m, 8) Flumserberg 1850 m, 9) Gamserrugg 2060 m, 10) Pizol 2215 m, 11) Hörnli 2440 m. The triangle denotes the city of Zürich (47°22'N, 8°31'E).

season length were computed: one index uses the date at which 11°C was exceeded for the first time. This date roughly corresponds to the initiation of postdiapause embryonic development, which is inhibited at temperatures below ca 11°C (Wingerden et al. 1991). The second index uses the cumulative degree hours above 14°C between the first appearance of larvae at each site and the end of the year. This approximates the season length for larvae and adults. 14°C was chosen based on a study by Hilbert and Logan (1983), because postembryonic development thresholds were unavailable for the species. However, grasshoppers are known to increase body temperature by basking (Begon 1983, Chappell 1983). Hence, the latter index must be viewed as a relatively crude, but still informative, estimate of the thermally effective season length.

Field phenologies were studied at the same sites and in the same year as the temperature records. Each site was visited in regular intervals of six to eleven days over the growing season. We censused by direct observation along transects, noting the stage (larval instars 1–4, adult) of each grasshopper. (The insertion of an additional larval instar reported from other gomphocerine grasshoppers (references in Ingrisch and Köhler 1998), occurred neither in the field nor laboratory.) Although males reach adulthood slightly earlier than females in this species, the sexes were pooled post hoc for simplicity. This did not influence the results substantially. As 2002 was a rather cool and cloudy year and 2003 was particularly sunny, we also checked the stage composition at site 1 in late June and site 10 in mid July 2003. These snapshots during the second year allowed a comparison of phenologies between climatically rather different seasons.

Breeding techniques and laboratory experiments

To establish breeding populations, ca 14 individuals of each sex were caught at the beginning of the reproductive period at each of the eleven sites. The populations 2, 5, 7 and 10 were sampled in 2001, all others in 2002. The animals were kept in groups in cages in a greenhouse under natural photoperiods until death. Field-cut grass (largely of *Dactylis glomerata* and *Agropyron repens*) was provided as food. Egg pods were collected twice a week as they were laid, put in plastic vials containing moist vermiculite, and incubated at 25°C for 35 d which allows the embryos to reach the diapause stage (Wingerden et al. 1991). After this, the clutches were stored at 5°C.

Postdiapause embryonic development time was studied in a climate chamber set to a photoperiod of 14 h at 27°C. Night temperature was 8°C. All eggs had spent at least three month at 5°C, which is enough to break diapause (Ingrisch and Köhler 1998). The vials were

inspected twice daily for newly hatched larvae, until no further hatch occurred. Individual hatch dates were noted and converted to degree hours with 11°C as threshold. We tested clutch medians in a general linear model (GLM), with study year as a fixed factor and altitude of origin (=populations) as a continuous covariate. Effective sample size varied between 18 and 79 clutches per population. To verify the robustness of our 27°C results, a subset of the clutches laid in 2002 was incubated at 19°C, but otherwise treated and analyzed in the same way. Here, sample size varied between 14 and 48.

To investigate larval development time, hatchlings were immediately transferred to another climate chamber with a 16 h photoperiod at 32°C and a night temperature of 10°C. This experiment was conducted with the seven 2002 populations only. Larvae were kept clutchwise in plastic containers (19 cm high, 8 cm in diameter) in groups of six at most. Small pots with a grass mixture provided food. Adult emergence was checked twice daily, and individual degree hours for larval development were determined using 14°C as threshold. We analyzed clutch medians using GLM. Altitude was entered as a covariate, and sex as a fixed factor, since the sexes differed in development time.

To assess diapause stages, ten random clutches from each of six populations (1, 2, 4, 7, 8, 9) were removed from the cold. The outer layer (chorion) of every single egg in the clutch was scraped off with a fine blade under a stereomicroscope so that the embryo could be seen and assigned a developmental stage. We used the classification system of Cherrill (1987), which divides the continuous process of differentiation to the fully developed embryo into twenty discrete morphological steps. Based on individual eggs, the clutch median stage was determined and treated as one data point. Differences between populations were tested using one-way ANOVA and a distribution-free Kruskal-Wallis test. All statistics were performed with SPSS 11.1.

Results

Temperature regimes

Daily mean temperatures of the top soil layer display a sharp decline with altitude (Fig. 2). Over the summer months, mean temperatures at 2215 m remain ca 7°C below those at 410 m. Moreover, snow cover maintains spring temperatures around zero at the high elevation sites, most dramatically at 2215 m. Indeed, the very first hourly temperature record above the estimated embryonic threshold of 11°C occurs as late as on the 31 May at 2215 m (Table 1). At the low elevation sites this threshold is exceeded almost three month earlier. Season length estimated as degree hours above 14°C shows a more than tenfold reduction from 410 m to 2215 m

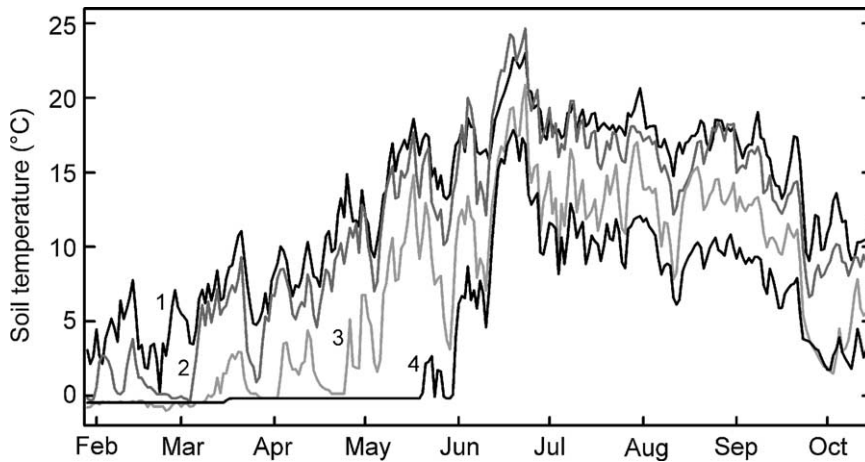


Fig. 2. Daily mean temperatures during the 2002 season at altitudes of 410 m (1), 1055 m (2), 1610 m (3) and 2215 m (4).

altitude (Table 1). Hardly any hourly records above 14°C were made after the end of August at the highest site. Roughly speaking, postembryonic development was possible during seven months at low altitude, whereas only three months were available at the highest site in 2002.

Field phenologies

The phenology curves in Fig. 3 indicate a marked delay in the emergence of first instar larvae at the high elevation sites, where the first hatchlings appeared three (1610 m) and seven (2215 m) weeks later than at the lowest location. The delay carries over to the adults: the graphically estimated dates at which each population reaches an adult frequency of 75% are 26 June (410 m), 31 June (1055 m), 23 July (1610 m) and 19 August (2215 m). Consequently, adult emergence at the highest site is delayed by almost two months compared to the lowland site. During the 2002 season lowland grasshoppers had already started reproducing when first instar larvae just started hatching at high altitude. In accordance with the temperature regimes, the difference in phenology between the sites at 410 m and 1055 m is small.

The comparison of 2002 (cool year) and 2003 (warm year) reveals a small difference in the low elevation phenology (Table 2). The greatest majority of the 410 m

population reaches adulthood by late June in both years. At 2215 m, however, the phenological difference between the two seasons is much larger. Clearly, the high altitude grasshoppers are delayed in both 2002 and 2003 relative to the lowland, but the phenological delay is more pronounced in the cooler year of 2002.

Laboratory experiments

There is a clear relationship between embryonic development time in the laboratory at 27°C and a population's altitude of origin (Fig. 4): high altitude embryos complete development faster, resulting in earlier hatching of the first instar larvae ($F_{1,431} = 50.9$, $p < 0.001$). However, the maximal difference between populations in development time amounts to some ten percent only. Expressed in real time, the population averages declined from 14.1 to 12.3 d. The year factor is also significant because temperature conditions differed slightly between the years (different climate chamber types; $F_{1,431} = 40.5$, $p < 0.001$). Faster development of the high altitude embryos was also found at the lower experimental temperature of 19°C. The correlation of population averages of embryonic development time at the two incubation temperatures yields coefficients of 0.85 (Pearson's r , $p = 0.015$) and 0.93 (Spearman's rank, $p = 0.003$).

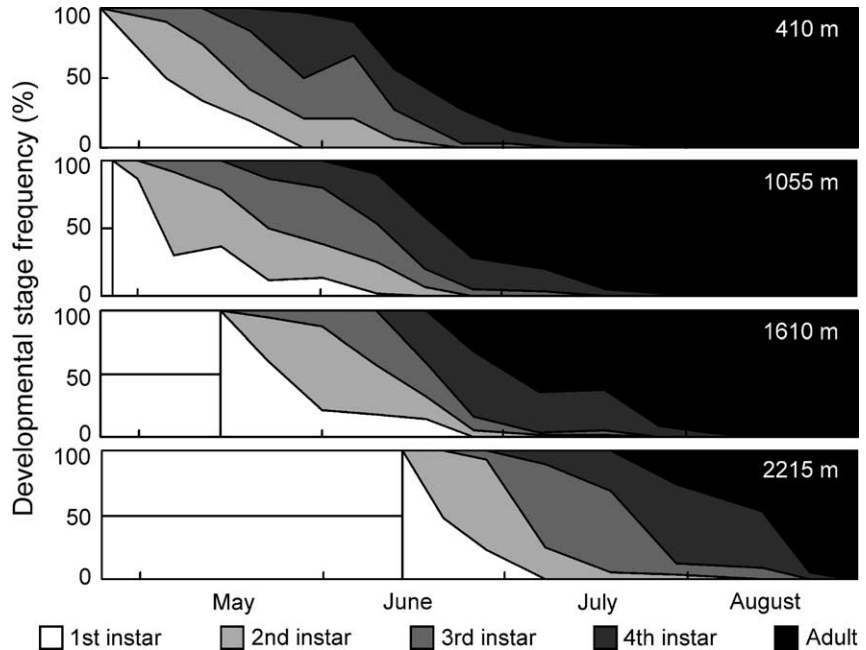
The duration of development through all larval instars to adults clearly gets shorter with altitudinal origin (Fig. 5; $F_{1,223} = 51.9$, $p < 0.001$), similar to embryonic development. As in the field, males always reach adulthood earlier than females ($F_{1,223} = 16.1$, $p < 0.001$), but the altitudinal response is similar in the sexes, as indicated by a nonsignificant interaction ($F_{1,223} = 1.3$, $p = 0.26$). Again, the difference between the fastest and slowest population is only about ten percent. In real time, the population averages for larval development ranged from 23.6 to 20.9 d in males and

Table 1. Indices of the 2002 season length at four altitudes, based on hourly temperature records at 1 cm soil depth.

Altitude (m)	Date of first record >11°C	Degree hours >14°C*
410	8 March	12536
1055	8 March	10019
1610	5 April	3182
2215	31 May	904

* From the onset of larval hatch to the end of the year.

Fig. 3. Field phenologies of *O. viridulus* at four altitudes during the season of 2002. The vertical line represents the first observation of hatchlings.



from 25.2 to 22.3 d in females for low and high altitude, respectively.

The stage of embryonic diapause does not significantly differ between the populations, and no altitudinal trend is evident (Fig. 6; ANOVA $F_{5,54} = 1.34$, $p = 0.26$; Kruskal-Wallis $\chi^2_5 = 8.09$, $p = 0.15$). In all *O. viridulus* populations studied, the vast majority of embryos diapauses at developmental stage nine, which corresponds to stage IVd of Cherrill (1987). The embryos are then arrested just before the onset of embryonic rotation. Most clutches contained some retarded eggs, but no single embryo developed further than stage nine.

Discussion

Our laboratory study documents increasing rates of embryonic and juvenile development in *O. viridulus* with increasing altitude. As a consequence, high altitude grasshoppers attain adulthood in shorter time than their low altitude counterparts when grown in a common environment. In contrast, the diapause stage, another

Table 2. Frequency (%) of *O. viridulus* instars in the years 2002 and 2003 at low and high elevation. Note that the two populations were censused on different dates.

	410 m, late June		2215 m, mid July	
	2002	2003	2002	2003
2nd instar	—	—	21	—
3rd instar	3	—	64	9
4th instar	18	3	15	31
Adult	79	97	—	60

key determinant of phenology, shows no difference among the populations. The field work indicates a time constraint on the life cycle of high altitude animals. The cooler high elevation temperature regimes substantially delay larval hatch and adulthood. In a cloudy year like 2002, the reproductive life span of alpine grasshoppers is thus severely truncated and reproductive success very poor. Moreover, a considerable fraction of the produced eggs may fail to reach the overwintering stage due to insufficient late season heat. This was shown to entail delayed hatching in *Chorthippus brunneus* (Cherrill and Begon 1991) and survival costs in *Camnula pellucida* (Pickford 1966). Certainly, cool and cloudy years are severe selection events at the species' upper range margin. Only during particularly sunny seasons like 2003 is the reproductive period sometimes terminated

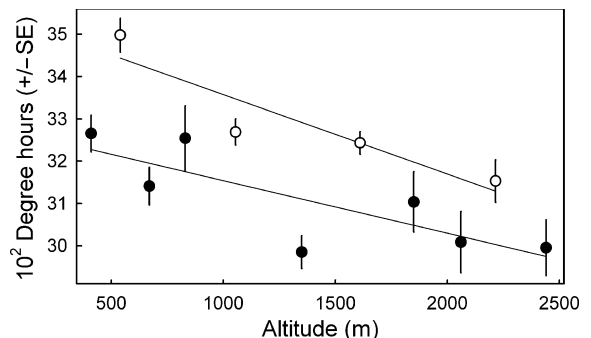


Fig. 4. Physiological time required by *O. viridulus* populations from different altitudes for postdiapause embryonic development. Data from 2002 (○) and 2003 (●). Degree hours were calculated using 11°C as threshold.

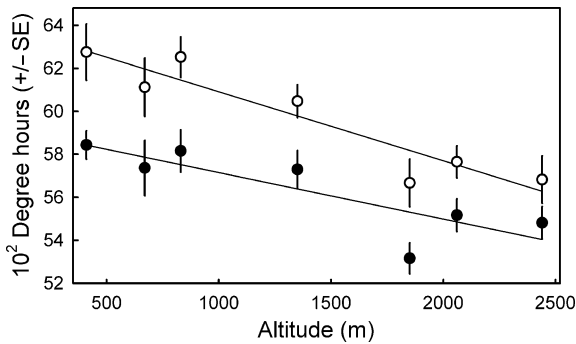


Fig. 5. Physiological time required by female (○) and male (●) grasshoppers from different altitudes for larval development. A threshold of 14°C was used for calculation.

by intrinsic senescence at both low and high elevation. Thus the variance in the available season length increases with altitude.

Under such a seasonal time constraint, annual organisms face the problem of optimally allocating time to development and reproduction. Life history models predict that decreased season length will favor faster development and hence decreased time to maturity (Cohen 1976, Roff 1980, 2002, Rowe and Ludwig 1991, Abrams et al. 1996). In *Omocestus viridulus* with its wide altitudinal distribution, therefore, we expected differences in traits determining postdiapause development time. The higher rates of development exhibited under laboratory conditions by the alpine populations thus conform well to the theoretical prediction. A genetic basis to the acceleration of development is strongly suggested because, firstly, maternal influence on offspring embryonic development appears negligible in the related *Chorthippus parallelus* (Köhler 1983). Secondly, our field records indicate that the temperatures used in the laboratory may be experienced by all populations in the field. Absorption of solar radiation may allow even

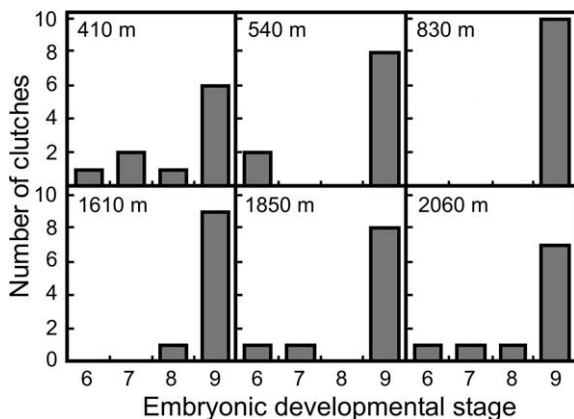


Fig. 6. Embryonic developmental stage at diapause in *O. viridulus* populations from six altitudes. Plotted are clutch medians (N = 10 per population).

high altitude larvae to rise body temperature well above 32°C. Furthermore, embryonic development rates were found to increase with altitude at incubation temperatures of both 19°C and 27°C. Strong genotype by environment interactions are thus excluded. For these reasons we suggest that the observed developmental differences are robust and reflect an adaptive strategy. Increased embryonic and larval development rates allow high altitude animals to reach maturity relatively faster, and hence prolong reproductive life span when time is short. The hypothesis of within species life history differentiation on a small spatial scale is thus confirmed. Apparently the level of gene flow between the *O. viridulus* populations is too low to counteract local adaptation.

Omocestus viridulus agrees well with some other ectotherms in which differentiation of development along gradients in season length has been documented (Masaki 1967, Berven and Gill 1983, Dingle et al. 1990, Ayres and Scriber 1994, Telfer and Hassall 1999). The shortening of development time proves a common adaptive response to seasonal time constraints. Intraspecific differentiation in traits related to phenology may be quite frequent in annual ectotherms with relatively long development times covering wide geographic ranges. However, our field surveys make it clear that the cool climates at high elevation retard grasshopper phenologies despite higher intrinsic rates of development in those populations. Thus, the high elevation grasshoppers are only partly able to compensate the delaying environmental influence on time to adulthood. This agrees with the relatively modest level of differentiation found in the laboratory. As the genetic response along the altitudinal gradient is opposed to the phenotypic response to the environmental conditions, *O. viridulus* provides an example of countergradient variation (Conover and Schultz 1995). A merely phenotypic comparison of development times within the species would have failed to demonstrate altitudinal differentiation.

At the proximate level, increased development rates may be associated with metabolic temperature compensation (Danks 1987). Hadley and Massion (1985) for example report increased metabolic rates in high altitude populations of the grasshopper *Aeropedellus clavatus*. Likewise, latitudinal differences in metabolism were found in the butterfly *Papilio canadensis* (Ayres and Scriber 1994). However, physiological traits of *O. viridulus* populations have not been compared so far.

A question arising from the observed patterns is why higher intrinsic rates of development did not evolve in the lowland populations. What could be the disadvantage of a similarly rapid development as at high elevation? On the one hand, adverse climatic conditions early in the season are likely to select against precocious

larval emergence. Carrière et al. (1996), for example, demonstrate a mortality cost associated with precocious larval hatch in *Gryllus pennsylvanicus*, due to unfavorable temperature conditions. Furthermore, trade-offs with other fitness components could maintain developmental rates below the physiological potential exhibited by the alpine populations (Schluter et al. 1991, Stearns 1992, Roff 2002). For instance, Tatar et al. (1997) found increased senescence in *Melanoplus sanguinipes* grasshoppers from high elevation sites compared to the slower developing low altitude animals. Likewise, given that juvenile development time, adult size, and fecundity are often correlated positively (Roff 1980, 2002, Rowe and Ludwig 1991, Honek 1993), a shortened juvenile development will negatively affect fecundity. According to Orr (1996) this is the case in *M. sanguinipes*. Most probably, elevated rates of development bear fitness costs and are selected against in the absence of a seasonal time constraint on the life cycle, as is the case at low elevation. However, low altitude seasons appear still too short for two generations, as the species exhibits an annual life cycle throughout its range.

Besides embryonic and larval development rates, the stage of overwintering strongly determines time to adulthood. Central European grasshoppers of the gomphocerine subfamily are believed to show an obligatory diapause during embryonic development. According to some studies, the dormant stage is inserted shortly before embryonic rotation (Köhler 1991, Ingrisch and Köhler 1998). This stage has been designated IVd by Cherrill (1987). However, geographic variation in diapause stage within an insect species is possible in principle (references in Tauber et al. 1986), but has not been investigated to date in any European grasshopper. In *O. viridulus* we found no such altitudinal differentiation: in all populations, most clutches mainly contained embryos arrested at the aforementioned stage, and no embryo developed further. Thus, the species displays an obligatory diapause and is uniform with respect to the stage of dormancy, conforming to other members of the subfamily. This finding stands in striking contrast to other orthopteran studies, which document intraspecific variation in embryonic diapause stage and/or expression along gradients in season length (Mousseau and Roff 1989, Groeters and Shaw 1992, Tanaka 1994, Dingle and Mousseau 1994, Bradford and Roff 1995). The catantopine grasshopper *Melanoplus sanguinipes*, for example, occurs from sea level to above 3800 m (Chappell 1983) and displays enormous variation in embryonic diapause stage within its North American range. High elevation populations overwinter almost completely developed and attain the hatching state at low heat sums. This is interpreted as an effective means to decrease postdiapause development time under short seasons (Dingle et al. 1990, Dingle and Mousseau 1994). In *M. sanguinipes*, adult emergence at above 2600 m and at sea level

happens roughly at the same time! Not surprisingly, another catantopine, *M. frigidus*, is the highest reaching species in the Alps (Carron 1996). This grasshopper subfamily illustrates the importance of flexibility in the overwintering stage for altitudinal adaptation. In this light, the lack of variation in the stage of diapause within *O. viridulus* likely represents a phylogenetic constraint (Gould 1989, Stearns 1992, Schlichting and Pigliucci 1998) to altitudinal range expansion. The stage of dormancy as a conserved trait within the gomphocerine lineage precludes tuning of development in a way expected to be optimal under seasonal time constraints. However, this has to be confirmed by investigating other, closely related species.

To summarize, *O. viridulus* exhibits altitudinal differentiation in development as an adaptive response to selection imposed by local climates. However, the potential for altitudinal adaptation is limited by the invariant stage of overwintering diapause, probably indicating a phylogenetic constraint within the gomphocerine grasshopper lineage. As a consequence, the degree of climatic compensation displayed by field populations along the altitudinal gradient is rather low as compared to other ectotherms.

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