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Pre-winter larval activity and feeding behavior of *Erebia aethiops* and *E. cassioides* in Austrian Alps

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Abstract: Freshly hatched larvae represent critical but little studied phase in insect development. In butterflies inhabiting seasonally harsh environments, such as mountains of temperate regions, the larvae have only short time available for feeding before entering diapause. In the species rich genus *Erebia*, post-diapause larvae activate and feed exclusively in evening and late night hours, whereas the diurnal schedule and modifying effects of weather of pre-diapause larvae are practically unknown. Using captive observation with a transplant between alpine (2000 m) and mountain (800 m) altitudes, we studied larval activity of two species, alpine *Erebia cassioides* and lower-altitude *E. aethiops*, in Austrian Alps. Both species activated and fed both during day time and after the sunset, contrasting with the situation in post-diapause larvae. Both activity and feeding were strongly and species-specifically affected by temperature, cloudiness and humidity. Additionally, the lower-altitude *E. aethiops*, but not the alpine *E. cassioides*, restricted activity and feeding in the alpine altitude, indicating that some factors particular for alpine environments, possibly increased UV load or reduced air pressure, may limit the ability of this mountain species to develop above its vertical distribution limit.

Key words: alpine habitats; altitude; diapause; larval ecology; diurnal rhythm; Lepidoptera; Satyrinae

Introduction

Butterflies from the genus *Erebia* Dalman, 1816 form a diverse Holarctic group, containing more than one hundred species worldwide (Tennent 2008). Most of them are cold-adapted, inhabiting mainly northern and mountain areas with only a few exceptions adapted to warmer environments. The genus is a subject of many phylogeographical and phylogenetical studies (e.g., Schmitt et al. 2006, 2016; Schmitt & Haubrich 2008; Pena et al. 2015). Recently, concerns with climate change encouraged biologist to study how these cold-adapted butterflies cope with changing environment (Scalercio et al. 2014; Konvička et al. 2016).

In this context, biology of larval stages plays an important role, due to their limited mobility and, compared to adults, relatively long duration. This makes them more sensitive to microhabitat conditions (cf. Fartmann & Hermann 2006; Stuhldreher & Fartmann 2015), which are especially important in harsh and unpredictable mountain climates that limit the time available for feeding activity (Parmesan et al. 2000). For example, dormant *Erebia* larvae of closely related species may differ in cold hardiness strategies so that, counter-intuitively, species inhabiting lower altitudes are cold-harder than the alpine ones. This is probably due to a better winter isolation of alpine habitats by snow, which protect the larvae from extreme frosts (Vrba et al. 2012). In contrast, adults are adapted to the rapidly changing alpine weather owing to their excellent thermoregulation ability (Kleckova et al. 2014; Kleckova & Klecka 2016).

Biology of *Erebia* larval stages is remarkably little studied, probably due to their difficult detectability in field. The larvae feed on grasses and hibernate in early stages within grass tussocks (Sonderegger 2005). Some of the species exhibit semivoltine life cycle, hibernating as the penultimate instar for the second time (Wipking & Mengelkoch 1994). The small pre-diapause larvae may reportedly feed during the day while post-winter larvae should be night-active, although exceptions were observed (Sonderegger 2005). Detailed information about diurnal activity profiles and the influence of environmental conditions on young prehibernation instars are lacking. To fill this gap, we studied autumn larval activity and behavior of two related *Erebia* butterflies, differing in preferred habitat and altitudinal distribution.

Material and methods

Species studied

Erebia aethiops (Esper, 1777) represents a lower-altitude species. Its Eurosiberian distribution ranges from Scotland through Central and Eastern Europe to western Siberia (Tolman & Lewington 1997); the altitude range is from sea level to ca 2000 m a.s.l., with Central European optimum below 1000 m a.s.l. (e.g., Slamova et al. 2013). It inhab-

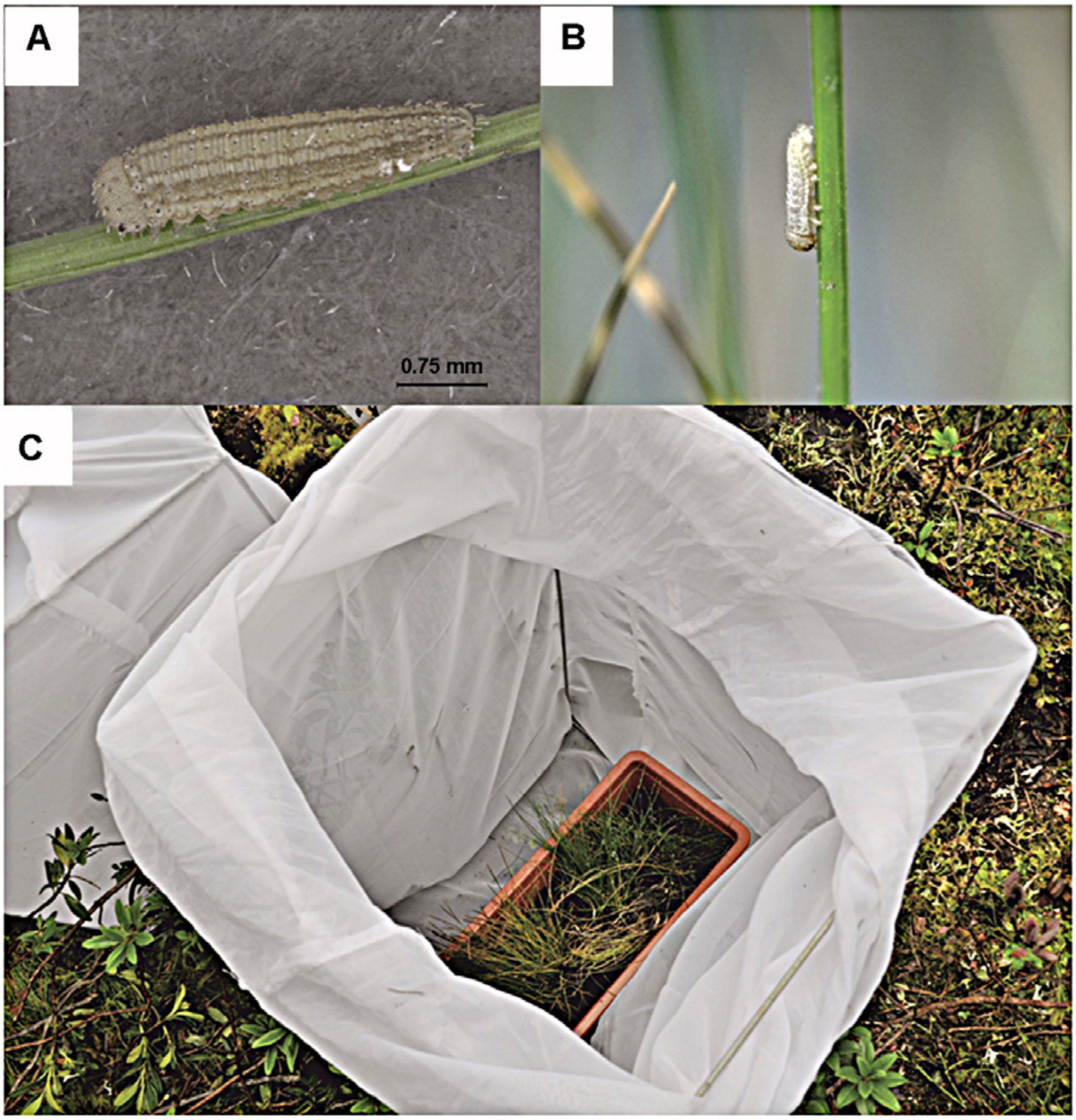

Fig. 1. Photographs showing *E. aethiops* first instar larva with scale (A); *E. cassioides* first instar larva active at upper part of a grass blade (B); and the outdoor rearing facility (C).

its sparse forests and grassy woodland clearings. The larvae overwinter in the second instar (Sonderegger 2005).

Erebia cassioides (Reiner & Hochenwarth, 1792) represents an alpine species. It belongs to the taxonomically difficult *Erebia tyndarus* complex. *Erebia cassioides* is distributed in Eastern Alps and Apennines at altitudes from 1600 to 2600 m a.s.l., populations from Western Alps and Balkan Peninsula are recently considered to be separate species (Schmitt et al., 2016). It inhabits grassy and rocky slopes around and above the timberline (Tolman & Lewington 1997); the larvae overwinter in the first or second instar (Sonderegger 2005).

Captive observation

To obtain freshly hatched larvae (Figs 1A, B), we captured 10 fertilized females of each species in Oetztal valley, Austrian Alps (Tirol). *Erebia aethiops* females were captured near Haiming, 800 m a.s.l. (47°16′ N, 10°52′ E), *E. cassioides* females near Hochgurgl, 2200 m a.s.l. (46°54′ N, 11°3′ E). Captured females were allowed to oviposit in plastic boxes (20 × 20 × 10 cm). To stimulate oviposition, we placed a mixture of locally occurring grasses into the box. Additionally, we fed the females with a 5% sugar solution to increase their lifespan and the number of eggs laid.

Freshly hatched larvae were placed to outdoor rearing facilities (Fig. 1C) on August 17, 2014. These were wired cages (50 × 50 × 100 cm) covered by mesh. Each cage contained a flower pot with planted grass tussocks collected from the localities of capture. These cages were placed outdoors to semi-shaded conditions in two locations differing in altitude and roughly representing the altitudes of origin of both species.

The first location was near Haiming, 800 m a.s.l., at the site where *E. aethiops* females were captured. The second was located near Kühtai, 2000 m a.s.l. (47°13′ N, 11°0′ E); *E. cassioides* adults were observed there. 150 freshly hatched larvae of each species were placed into each location to compare their diurnal activity profiles and behavior in optimal

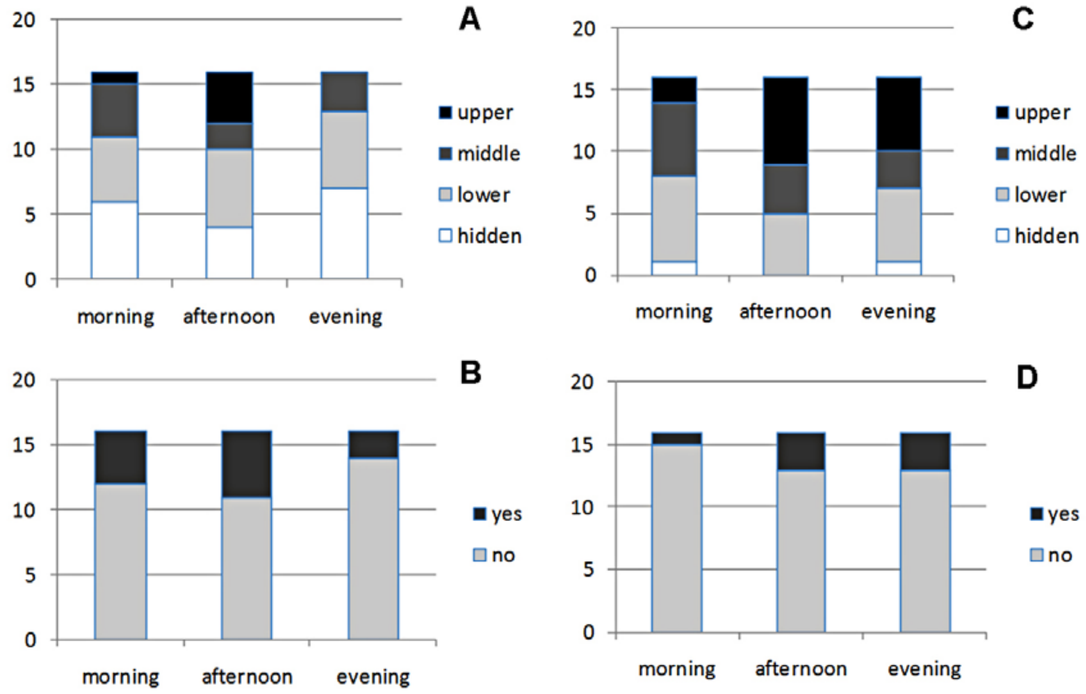

Fig. 2. Numbers of observations of different activity categories (larval positions within grass tussocks) and feeding records in various times of a day. A, B – *Erebia aethiops*; C, D – *E. cassioides*.

and non-optimal altitude. At each altitude, larvae of each species were divided into two cages. At both altitudes, cages were controlled three times a day (morning: 9–10 h, early afternoon: 13–14 h, evening: 20–21 h) for two four-day periods: August 29 – September 1 and September 11 – September 14. Note that the evening controls were after the sunset and thus corresponded to a presumed peak activity of post-diapause larvae.

Because the larvae are very minuscule (ca 3 mm), it was not possible to follow them individually. Therefore, we recorded average positions of the whole larval groups at the grass tussocks. When resting, the larvae hide inside grass tussocks while under suitable conditions, they move to upper parts and consume grass blades from the tips downwards (Sonderegger 2005). The average positions were: *hidden*, *lower*, *middle*, and *upper* (parts of the leaves). We also recorded whether a feeding was visible (*yes*/*no*). In addition, the following variables were recorded: *time* (morning, afternoon, evening), *cloudiness* (1 – sunny; 2 – partly cloudy; 3 – cloudy; 4 – overcast, light rain), momentary air *temperature*, and visually assessed *humidity* of grass tussocks (1 – dry, 2 – tips of the grass dry, lower parts wet, 3 – wet, 4 – very wet).

Following this captive rearing observations, the larvae were transported to the laboratory, allowed to enter diapause and used in experiments not reported here.

Statistical analyses

All analyses were performed separately for the two species, in order to elucidate differences in their feeding and activity patterns.

For feeding, a two-state factorial variable, we used generalized linear models with binomial distribution of errors computed in R (R Development Core Team 2016) and evaluated using the Akaike information criterion (Akaike 1974). After constructing a null model, we fitted models for all possible separate predictors, including their second-degree polynomials. Next, we manually constructed a final model, which best fitted the data based on combining all predictors at hand and their interactions.

Activity (i.e., the larval positions within the grass tussocks) was coded as four-states ordinal response variable, and the effects of time, weather and altitude were again assessed using the general linear models, this time with Gaussian distribution of errors.

Results

Erebia aethiops larvae were most frequently observed in middle and lower parts of the grass tussocks, except for afternoons, when they sometimes climbed to upper parts of the tussocks (Fig. 2A). Regardless time of day, the larvae were hidden in about a third of all observations. Records of feeding were more frequent in mornings and afternoons than in evenings (Fig. 2B). *Erebia cassioides* larvae were generally more active, they were more frequently observed in upper and middle parts of tussocks (mainly in afternoons and evenings), and there were only few observations, all in mornings and evenings, when they were hidden (Fig. 2C). Feeding was observed in all three time periods, with equal numbers of afternoon and evening records and fewer morning records (Fig. 2D).

The lower temperature threshold for feeding was 8.2 °C for the lower-altitude species *E. aethiops* and 5.8 °C for the alpine species *E. cassioides*. For both species, there also appeared an upper temperature threshold for feeding: 17.8 °C for *E. aethiops* and 16.5 °C for *E. cassioides* (the highest air temperatures detected were 23 °C in 800 m and 19.5 °C in 2000 m altitude).

In the regression models for feeding (Table 1), the best-fitting single-term predictor for *E. aethiops* was

Table 1. Results of glm regressions relating prediapause *Erebia* larvae feeding (binary variable) and activity (positions within grass tussock, four-state ranked variable) to time of day, weather predictors and altitude (two states: 800 and 2000 m a.s.l.), as observed in outdoor rearing facilities. See Results for directions of the responses.

Erebia aethiops	Dev	df	AIC	*Erebia cassioides*	Dev	df	AIC
FEEDING							
~ null	51.67	47	53.67	~ null	39.88	47	41.88
~ time	50.9	1, 46	54.96	~ time	38.86	1, 46	42.86
~ cloudiness^2	47.48	2, 45	53.48	~ cloudiness^2	31.41	2, 45	37.41
~ humidity^2	44.73	2, 45	50.73	~ humidity	33.69	1, 46	37.69
~ temperature^2	41.38	2, 45	47.38	~ temperature	39.63	1, 46	43.63
~ altitude	45.52	1, 46	49.52	~ altitude	38.33	1, 46	42.33
~ *humidity*^2 + *temperature*^2 + *humidity*^2*temperature*^2	*17.56*	*8, 39*	*35.56*	~ *time* + *cloudiness*^2 + *time*cloudiness*^2	*21.38*	*5, 42*	*33.38*
ACTIVITY							
~ null	45.92	47	138.1	~ null	39.98	47	131.4
~ time^2	42.75	2, 45	138.7	~ time^2	37.44	2, 45	132.3
~ cloudines^22	32.16	2, 45	125.0	~ cloudiness	39.34	1, 46	132.7
~ humidity	40.92	1, 46	134.6	~ humidity	36.01	1, 46	128.4
~ temperature	43.62	1, 46	137.6	~ temperature	26.45	1, 46	113.6
~ altitude	33.92	1, 46	125.5	~ altitude	38.96	1, 46	132.2
~ *altitude* + *cloudiness*^2 + *altitude*cloudiness*^2	*20.55*	*5, 42*	*109.5*	~ *humidity* + *temperature* + *altitude*	*22.13*	*3, 44*	*109.1*

Explanations: Multiple-regression final models are in *italics.* Dev – residual deviance of the respective model, df – the models degrees of freedom, AIC – Akaike information criterion.

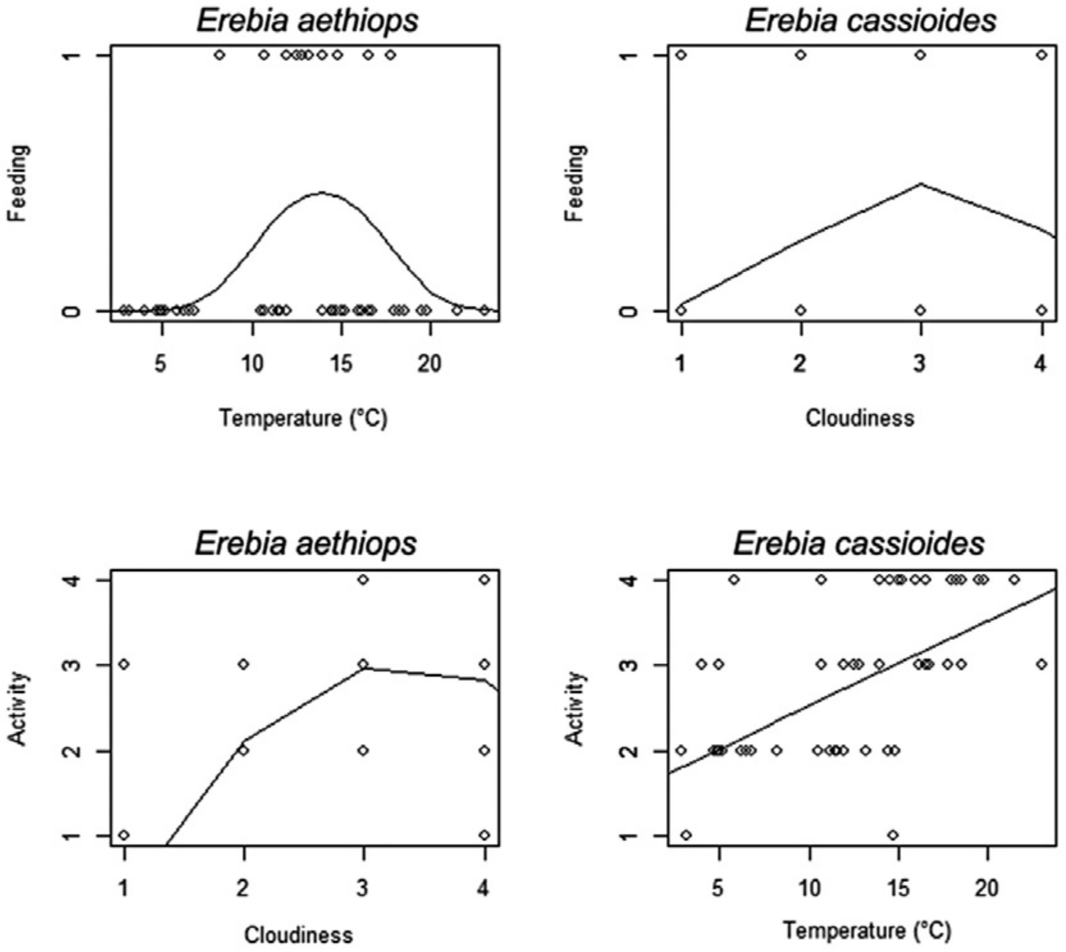

Fig. 3. Graphic expression of the best-fitting single-term predictors in glm regression models for *Erebia* larvae feeding (1 – yes, 2 – no) and activity (1 – hidden, 2 – lower, 3 – middle, 4 – upper parts of the leaves). The lines show glm predicted values, best-fitting predictors are displayed on x-axis (cloudiness: 1 – sunny; 2 – partly cloudy; 3 – cloudy; 4 – overcast, light rain).

second-degree polynomial of air temperature (explaining 19.9% of the variation), corroborating the existence of lower and upper temperature thresholds for feeding (Fig. 3). Other considerably weaker predictors fitting the data were second-degree polynomial of humidity (13.4%), and altitude (11.9% – fewer feeding observations at 2000 m). Time had no effect. The final model contained humidity, temperature (in a domed manner) and their interaction. For feeding of *E. cassioides*, second-degree polynomial for cloudiness and humidity were almost equally good predictors (ΔAIC = 0.28), fitting 21.2% and 15.5% of the variation in the data, respectively, whereas time, temperature and altitude had no explanatory power. However, the final model contained time interacting with the second-degree polynomial of cloudiness.

In the models for activity, the two best-fitting single term predictors for *E. aethiops* were cloudiness, fitted as a second-degree polynomial (Fig. 3) and explaining 30.0% of the variation, and altitude, explaining 26.1% of the variation (ΔAIC = 0.50); further but much weaker predictor was humidity (10.9% of the variation). Neither time nor temperature had any explanatory effects. The final model contained altitude, a polynomial response to cloudiness, and the interaction term, suggesting that the response to cloudiness differed in 800 m and 2000 m altitude (Table 1). For *E. cassioides*, the best fitting single-term predictor was temperature, fitted linearly and explaining 33.8% of the variation; it was followed by humidity in a linear fit (9.9%). Time, cloudiness and altitude had no effect. The final model contained the two linear terms, temperature and humidity, combined with altitude.

Discussion

The prediapause larvae of two *Erebia* butterflies, one from lower altitudes and one with high alpine distribution, activate and feed independently on day time. This contrasts with the known situation in grown-up postdiapause larvae of this prevailingly alpine genus that activate and feed in evening and early night hours, between the Sun sets and the temperature becomes too low for activity (cf. Kuras et al. 2001; Sonderegger 2005). Rather than to time of day, activity of both species responded to weather conditions. However, while in the high alpine *E. cassioides* both feeding and activity responded mainly to weather, and altitude acted as a modifying predictor in multiple-regressions only, both feeding and activity of the lower-altitude *E. aethiops* was affected by altitude itself so that its larvae responded to weather differently within their native elevation of 800 m and when transplanted to 2000 m.

During our observations, we treated the larvae as whole groups, visually estimating their average positions on grass tussocks and presence/absence of feeding. A more rigorous option, keeping them in separate containers and recording their activity individually, would preclude observing them in as natural conditions as possible, in the environment of grass tufts, while minimizing handling disturbance. The prediapause larvae are tiny and fragile. Our approach sufficed for the original aim of the study, ascertaining the larval daily activity regimen. All other observations, unexpected while planning this study, should be viewed as conjectural and require further corroboration.

The difference between the crepuscular to nocturnal activity of postdiapause larvae and the diurnal activity of prediapause larvae is explicable by the time window available for larval feeding before the onset of autumn frosts, when the grass foliage becomes wilted and unpalatable. Presumably, the prediapause larvae have to utilise any moment with suitable weather for feeding. The evenings may be considerably cooler, affording shorter time for crepuscular feeding, in September than in June, when the bulk of postdiapause development occurs. The reason why grown-up Satyrinae larvae feed after the sunset is probably connected to defense mechanisms. Their external cuticle is glabrous, lacking protective hair and their grass diet does not contain sequestrable protective compounds (cf. Cizek et al. 2006). Then, crepuscular feeding protects them from avian predators, as well as mostly diurnally active parasitoids, such as Hymenoptera – Ichneumonoidea (Gauld 1986). In autumn, the threats from both birds and Hymenopterans are lower compared to late spring or early summer, presumably relaxing the constraints imposed in spring to feeding schedule. It is also likely that small pre-winter larvae are less visible (and less attractive) for the few avian predators present in alpine environments at that time of year.

The two species differed in weather requirements. The high alpine *E. cassioides* was able to feed under lower temperatures, in line with generally harsher conditions in its native environment. *E. aethiops* displayed an upper temperature threshold for feeding, whereas feeding of *E. cassioides* peaked under lower humidity and intermediate sunshine. The patterns for general activity were somehow different, both species were more active under higher temperatures and lower humidity, but in *E. aethiops* this was modified by cloudiness in a domed manner. As shown by Kleckova & Klecka (2016), adult *Erebia* display species-specific responses to weather. Apparently, this conjecture applies to prediapause larvae as well.

While altitude itself entered only a multiple regression model in *E. cassioides*, it had strong and independent effect on both feeding and activity of *E. aethiops.* In high altitudes with decreased air pressure, a lack of oxygen under high temperatures may set upper temperature thresholds for insect feeding (Hodkinson 2005). Whereas the alpine *E. cassioides* should be adapted to lower air pressures, too low air pressure may reduce activity of the lower-altitude *E. aethiops.* In addition, the domed effects of cloudiness on *E. aethiops* activity and feeding, and *E. cassioides* feeding, strongly suggest an influenced of ultraviolet radiation. Lethal effect of high UV radiation on early instar Lepidopteran larvae was recently illustrated on several moths species, such as *Ephestia kuehniella* Zeller, 1879 (Pyralidae) (Guven et al. 2015) and *Mythimna separata* Walker, 1865 (Noctuidae) (Ali et al. 2016). Normally, *E. kuehniella* would hardly experience high UV loads, as it develops inside in stored cereals. On the other hand, *M. separata* larvae share several life history traits with larvae of *Erebia*. They also develop on grasses, have glabrous cuticle and feed nocturnally (Sato et al. 1983), offering a good model for possible UV effects on *Erebia* larvae. It hence appears that prediapause *Erebia* larvae utilize any time of day for feeding and that higher temperatures stimulate their activity, but the lower-altitude *E. aethiops* is constrained by some factors specific to alpine altitudes: either high solar UV or low air pressure. It is possible that UV avoidance has contributed to the evolution of nocturnal feeding habit of larval *Erebia*, along with avoidance of predators. In addition, higher UV impact during the postdiapausal development (May – June), combined with the detected upper temperature threshold, may also contribute to different diurnal activity profiles in autumn and spring. Deciding between these effects is beyond the scope of this study.

Our study of prediapause larvae of two species of *Erebia* butterflies, members of a genus with remarkable radiation in alpine, boreal and arctic environments of Northern hemisphere, pointed to specific reactions to weather and altitude-related factors. Given the diversity of habitats in which individual *Erebia* species occur (Sonderegger 2005; Kleckova et al. 2014) and their ability to partition habitat use at relatively small scales (Kuras et al. 2000; Dinca et al. 2010; Polic et al. 2014), it is possible that strategies of prediapause larvae may be as diverse, as are the patterns of cold hardiness during diapause (Vrba et al. 2012; Stuhldreher et al. 2014), adult thermoregulatory activity (Kleckova & Klecka 2016) or population demography structures (Kuras et al. 2003; Polic et al. 2014). Minute differences in early larval instars preferences, such as those concerning temperature thresholds for activity, tolerance to UV radiation, or preference for specific shelters and their presence or absence within their habitats (e.g., rock crevices, tall or short grass tufts, etc.) may then contribute to delimiting species-specific altitude ranges. Freshly hatched larvae represent a short-lasting, relatively little studied but nevertheless critical developmental stage of Lepidoptera. Comparative studies of factors affecting their performance under varying conditions deserve attention by future research.

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