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Commentary

Increased ultraviolet-B radiation, climate change and latitudinal adaptation — a frog perspective

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According to a traditional view, organisms and populations inhabiting high latitudes are likely to be exposed to lower effective doses of potentially harmful solar ultraviolet-B radiation (UV-B) than those inhabiting lower latitudes. We challenge this traditional view by demonstrating that due to differences in phenology, populations occurring at high latitudes may actually be exposed to much higher effective doses of UV-B radiation than those occurring at lower latitudes. Related to this, we point out a possibly wide-spread interaction between climate change and ozone depletion which can effectively mask (or delay the appearance of) the negative effects of increased solar UV-B radiation on organismal fitness. These points are illustrated with examples from amphibians, which have been recently suggested to be particularly vulnerable for UV-B mediated fitness loss.

Introduction

The thinning of the stratospheric ozone layer during the last decades has increased the levels of ultraviolet-B radiation (UV-B, 280–315 nm) reaching Earth's surface, and this increase has been particularly pronounced at high latitudes (Madronich *et al.* 1998). Because mean yearly levels of UV-B radiation are lower at northern than at more southern latitudes — due to both a naturally thicker ozone layer and decreasing solar inclination towards the north — it has generally been assumed that organisms inhabiting northern latitudes may be particularly vulnerable to high levels of UV-B radiation (Caldwell *et al.* 1980, Barnes *et al.* 1987, Gehrke 1998). This generalisation is based on the assumption that the total effective doses of UV-B received by individuals or organisms at different latitudes follow strictly the latitudinal variation in total amounts of UV-B radiation reaching Earth's surface. While this is likely to be true for some organisms (e.g. mature

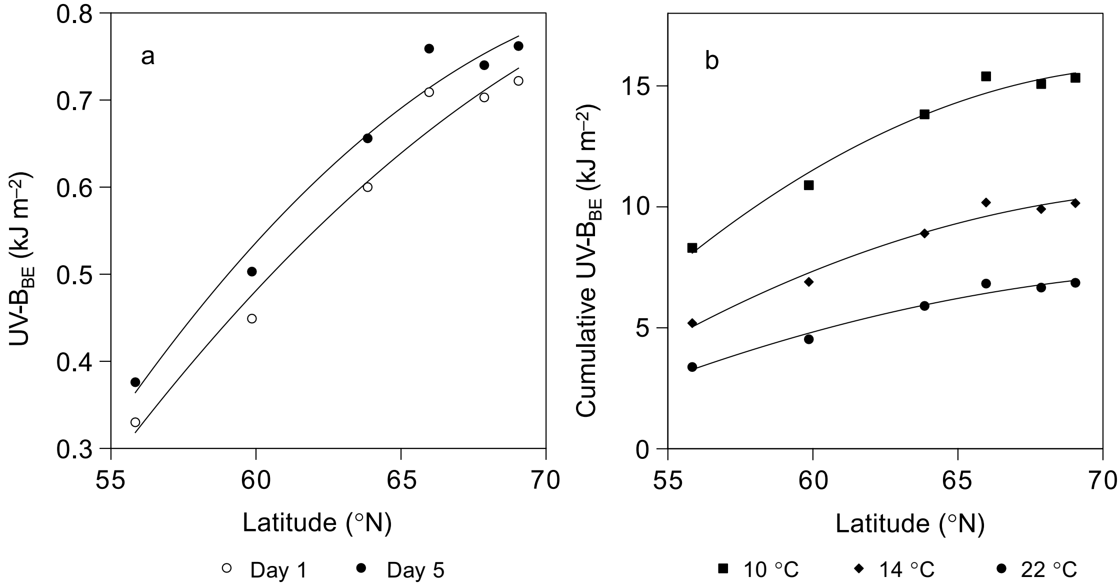

Fig. 1. Latitudinal trends in UV-B radiation doses experienced by common frog (*Rana temporaria*) embryos at different latitudes. (a) The amount of UV-B radiation at different latitudes in Sweden during the first five days of spawning. (b) Cumulative doses of UV-B radiation experienced by common frog embryos at different latitudes assuming three different developmental temperatures. Note that the effect of low temperature amplifies the UV-B radiation doses experienced by the northern frogs. The expected effective UV-B radiation doses were calculated using a program of Björn and Murphy (1985) and the DNA weighting function by Setlow (Green & Miller 1975) assuming clear sky conditions (note: the program accounts for geographical variation in the thickness of the ozone layer). Spawn initiation dates used to determine the UV-B doses are based on empirical data from six different populations along the depicted gradient in 1998 (Table 1). The length of the egg-stage at different temperatures, on which the calculations of cumulative doses are based on, were based on measurements of developmental rates of common frog eggs from Lund reared in three different temperatures in laboratory (10 °C = 19 days, 14 °C = 11 days, 22 °C = 9 days; A. Timenes Laugen, A. Laurila, & J. Merilä, unpubl.).

conifer trees), it has seldom been considered that the effective doses of UV-B radiation to which some other organisms are exposed to at high latitudes (even in the absence of ozone depletion) may actually greatly exceed those experienced by their conspecifics at more southern latitudes. Therefore, if adaptation to the local UV-B radiation regime has occurred, the expectation that sub-arctic and arctic organisms would be more vulnerable to UV-B radiation (AMAP 1998) may be mistaken.

Here, we argue that, while the view that organism inhabiting sub-arctic and arctic environments are exposed to smaller doses of UV-B radiation than those in more southern latitudes may be correct in the case of some taxa (e.g. adult stages of flowering plants), this expectation may be grossly erroneous in other instances, such as in the case of UV-B sensitive embryonic and larval stages of many aquatic animals. In fact, a number of logical arguments suggest that northern populations could be expected to be better adapted to cope with high levels of UV-B radiation than their more southern conspecifics. Related to this, we draw attention to a possible antagonistic interaction between recent ozone depletion and climate change on UV-B mediated fitness loss of natural populations.

Latitudinal variation in breeding time and effective doses of UV-B radiation

As an example of the scenario outlined above, we calculated the effective daily dose of UV-B radiation reaching different localities along a latitudinal gradient within Sweden during the early spawning season of the common frog (*Rana temporaria*; Fig. 1a). The calculations show that the effective daily dose of UV-B radiation increase rapidly until about 65°N, and somewhat less steeply thereafter (Fig. 1a). In fact, this exercise shows that the UV-B radiation dose in northern Sweden during the early spawning season is about twice that in southern Sweden (Fig. 1a), suggesting that the exposure of the UV-B sensitive embryonic stages of frogs (Blaustein *et al.* 1998) is much higher in the north than in the south. This pattern is the reverse of the commonly held view that northern populations of an organism are exposed to lower doses of UV-B radiation than those breeding at more equatorial latitudes (Caldwell *et al.* 1980). The higher doses of UV-B radiation received by frogs in the north are solely due to the fact that breeding time in the north is later than that in southern Sweden, and a later breeding time means higher solar inclination and longer day length, and therefore, higher doses of UV-B radiation (Table 1). We do not currently know whether frogs, or any other organism for that matter, from northern populations are more tolerant to UV-B radiation than those from southern populations. However, several studies have found evidence that ambient levels of UV-B radiation can cause severe embryonic mortality in amphibians (review in Blaustein *et al.* 1998), and hence, UV-B radiation may be an important abiotic selective factor shaping physiology and life histories of amphibians. If so, we should expect populations inhabiting higher latitudes to have evolved more efficient means (e.g. behavioural or/and physiological; Epel *et al.* 1999) of coping with higher doses of UV-B radiation than those from the south.

Another reason to expect that northern populations of organisms could be better adapted to cope with high doses of UV-B radiation relates to the general decrease in ambient temperature from south to north. Because many physiological processes are temperature dependent, growth and developmental rates of many organisms in the north are generally lower than those of their more southern conspecifics (Garland & Adolph 1991, Conover & Schultz 1995). Although the depressing effects of low ambient temperature can be partly counteracted by the evolution of faster developing and growing morphs in the north, these compensatory adaptations do not often fully compensate for lowered performance (e.g. Conover & Schultz 1995). Consequently, if the exposure time to UV-B radiation of sensitive juvenile stages is longer in the north, one could expect that northern populations have also been selected to better tolerate this radiation.

Relating to the scenario above, we also wish to point out that the conclusions emerging from the results presented in Fig. 1a are qualitatively similar to those resulting from summing UV-B radiation doses over the whole embryonic period in a given locality (Fig. 1b). In Fig. 1b we have calculated cumulative effective UV-B radiation doses at different latitudes by assuming three different developmental rates. The calculated effective doses are again an increasing function of latitude, which shows that the simple calculations above provide a good approximation of effective doses the different populations experience (Fig. 1b). Here too, it is clear that exposure to UV-B radiation in the north exceeds that in the south at all given temperatures because of the later initiation of spawn, but even more so if the ambient temperatures experienced by the embryos in the north tend to prolong their development as compared with that of those in the south. For exam-

Table 1. Descriptive data on localities and breeding times of frogs in these localities for which the amount of UV-B radiation received was estimated. Data for date of spawn initiation from different localities were collected in 1998. Solar inclination and day length are given for days when the spawning in given locality was initiated.

Locality	Latitude	Altitude (m)	Solar inclination	Day length (h)	Date of spawning
Lund	55°50´N	19	44°	12.9	1.4
Uppsala	59°52´N	50	42°	14.8	20.4
Umeå	63°51´N	15	44°	17.5	10.5
Ammarnäs	65°58´N	401	45°	18.3	25.5
Kiruna	67°52´N	425	44°	24.0	30.5
Kilpisjärvi	69°03´N	485	43°	24.0	5.6

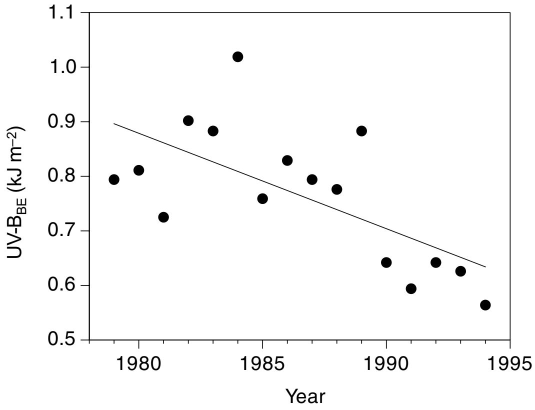

Fig. 2. Decrease in theoretical effective UV-B doses experienced by British natterjack toads (*Bufo calamita*) during 1979–1994 caused by earlier breeding dates. Note that the amount of effective UV-B radiation experienced by developing embryos has been reduced 29% during this time period solely due to earlier breeding times. The rate of ozone depletion required to counteract this trend would be 14%. Data for spawning dates from Beebee (1995). The depicted line is the slope of linear regression ($y = 35.503 - 0.017x$; $F_{1,14} = 10.7$, $P = 0.0056$).

ple, assuming a 4 °C difference in ambient temperature during development at 56°N and 69°N northern frogs would receive a UV-B radiation dose three times higher than those in the south (Fig. 1b). Hence, the view that northern ecosystems may be more vulnerable to increased levels of UV-B radiation is not necessarily as universal as the current literature leads to believe.

We should also point out that the observed increase in calculated estimates of effective daily doses of UV-B radiation towards the north are not qualitatively sensitive to assumptions about cloudiness. The number of sunshine hours, as determined from empirical observations, is roughly the same in both northern and southern part of the country, although coastal regions receive more sun (Raab & Wedin 1995). If the differences in amphibian breeding times in different parts of the country are taken into account, southern Sweden experiences fewer (ca. 170 hours in April) sunshine hours than northern Sweden (ca. 260 hours in June). Likewise, the number of cloudy and clear-sky days shows no clear north–south trends (Raab & Wedin 1995). Furthermore, the effects of clouds on UV and global radiation are known to differ (Kylling *et al.* 1996, Josefsson & Landelius 2000): clouds do not decrease UV radiation as much as global radiation, and if there is any solar elevation dependency in the effects of clouds, these must be small (Josefsson & Landelius 2000). More importantly, empirical measurements of UV-B radiation in five fixed points from Lund to Kiruna 1990–1995 (Josefsson 1996) showed the same increased trend of UV-B radiation towards the north (accounting for differences in the breeding time of amphibians) as depicted in Fig 1. In fact, the amount of UV radiation intercepted in Lund (25 200 J m^{-2}) in early April is roughly half of that in Kiruna in June (52 500 J m^{-2}; Josefsson 1996).

Climate change and ozone depletion interactions

Several recent studies have reported consistently earlier breeding times in various northern European animal species, including amphibians (Beebee 1995, Forchhammer *et al.* 1998). In concert with these observations, budburst and flowering times of many plant taxa have advanced during the last decades (Menzel & Fabian 1999). These changes in phenology have been attributed to higher spring temperatures, which may owe to large-scale climate changes (Jones 1994, Crick *et al.* 1997, Forchhammer *et al.* 1998, Przybylo *et al.* 2000). One consequence of the earlier spring is that organisms at northern latitudes will start their annual life-cycle not only earlier relative to calendar date, but also in relation to maximum UV-B radiation dose in their habitat. One potential consequence of this is that the effective UV-B radiation dose, to which organisms such as the developing amphibian embryos are exposed to, is actually decreasing faster than the increases brought by the depletion of the ozone layer. This is illustrated with a hypothetical example in Fig. 2. Here, we have used the data of mean spawning dates of natterjack toads (*Bufo calamita*) in England during 1979–1994, and calculated the expected UV-B radiation dose under clear sky conditions for each of the years. The trend suggested by this data is that the effective UV-B radiation dose at the start of spawning has decreased by about 29% during the last decades. The rate of ozone layer depletion required to 'counteract' this trend (using the Björn & Murphy (1985) model and the DNA weighting function by Setlow (Setlow 1974, Thimijan *et al.* 1978)) would be 14% during the same time. This suggests that climate change could effectively mask the potentially negative effects of increased UV-B radiation on amphibian development. The same may apply to plants flowering in early spring, and to any other organisms in which the most UV-B radiation sensitive stages are expressed in early spring. Likewise, in one of the localities depicted in Fig. 1a (Ammarnäs, 66°N), the spawning in mountain valleys (altitude 400 m) is initiated about two to three weeks earlier than in the mountain plateau situated a few kilometers away, but at an altitude of ca. 740 m. The difference in the daily UV-B radiation dose, due only to the difference in altitude, at the time spawning is initiated in the valley would be 2.4%. Because of the later spawning date in the higher population, the actual difference in the received daily dose between these closely situated populations is in fact 35%**.** The lesson from this exercise is that the negative consequences of increased UV-B radiation due to ozone depletion might be counteracted or even reversed by increased spring temperatures. If this was the case, two important ramifications emerge. The first one is related to our understanding of the impact of increased UV-B radiation on natural ecosystems, whereas the other one relates to questions about the design of experiments aiming to detect the impact of ozone depletion in nature.

Firstly, because of the climate–UV-B radiation interaction, the negative effects of ozone depletion in nature may go undetected for long periods of time. If animals and plants advance their breeding/flowering times in concert with temperature, they will be exposed to less UV-B radiation than they would experience in the absence of climate warming. As the increases in both levels of UV-B radiation (Madronich *et al.* 1998) and temperature (Hulme *et al.* 1999) are expected to be especially pronounced at the northern latitudes, available information suggests that such a scenario is plausible, if not highly likely.

Secondly, if the effects of ozone depletion and climate warming counteract each other in the fashion pictured above, detection of the biological consequences of ozone depletion in nature will require experiments where either temperature or UV-B radiation levels are manipulated. Non-manipulative experiments, albeit providing a good first step towards answering questions about actual impact of given UV-B radiation levels on biological systems are clearly insufficient if they do not account for temporal shift towards decreased UV-B radiation. In other words, they are vulnerable to erroneous acceptance of null-hypothesis of no effect of ozone depletion. For example, imagine a scenario under which a 10% ozone depletion in Uppsala in April leads to a 26% increase in a effective UV-B radiation over the next decade, and at the same time, increased spring temperatures lead to 8 days advancement of breeding time of amphibians per year. The consequence of this would be that the levels of UV-B radiation experienced by amphibians do not increase during this time. Clearly, under this scenario, point measures of impacts of UV-B radiation on amphibians in nature would not be expected to provide evidence for increased negative effects of UV-B radiation with time.

Conclusions

In conclusion, we challenge the widely held view that northern ecosystems, or species inhabiting high latitudes, would be generally more vulnerable to increased levels of UV-B radiation than their more southern conspecifics. Our examples show that, at least in the case of amphibian embryos, current (and historical) exposure to UV-B radiation in north has probably exceeded that of their more southern conspecifics. Whether this has led to evolutionary adaptations conferring higher UV-B radiation resistance in the north remains a challenge to future studies, but our calculations clearly demonstrate that this would not be unexpected. Furthermore, we have pointed out a possible interaction between climate change and ozone depletion, which might provide many organisms, such as amphibians, at least a partial escape from potential fitness loss caused by increased levels of UV-B radiation. However, such escape could be largely ephemeral, and more research is needed to evaluate the interactions between climate change and UV-B radiation on fitness in natural populations of plants and animals.

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