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SHORT COMMUNICATION

Glass buildings on river banks as "polarized light traps" for mass-swarming polarotactic caddis flies

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Abstract The caddis flies *Hydropsyche pellucidula* emerge at dusk from the river Danube and swarm around trees and bushes on the river bank. We document here that these aquatic insects can also be attracted *en masse* to the vertical glass surfaces of buildings on the river bank. The individuals lured to dark, vertical glass panes land, copulate, and remain on the glass for hours. Many of them are trapped by the partly open, tiltable windows. In laboratory choice experiments, we showed that ovipositing *H. pellucidula* are attracted to highly and horizontally polarized light stimulating their ventral eye region and, thus, have positive polarotaxis. In the field, we documented that highly polarizing vertical black glass surfaces are significantly more attractive to both female and male *H. pellucidula* than weakly polarizing white ones. Using video polarimetry, we measured the reflection-polarization characteristics of vertical glass surfaces of buildings where caddis flies swarmed. We propose that after its emergence from the river, *H. pellucidula* is attracted to buildings by their dark silhouettes and the glass-reflected, horizontally polarized light. After sunset, this attraction may be strengthened by positive phototaxis elicited by the buildings' lights. The novelty of this visual–ecological phenomenon is that the attraction of caddis flies to vertical glass surfaces has not been expected because vertical glass panes do not resemble the horizontal surface of waters from which these insects emerge and to which they must return to oviposit.

Keywords Caddis fly · *Hydropsyche pellucidula* · Polarization vision · Polarotaxis · Glass surface · Ecological trap

Introduction

It has been reported that various man-made, shiny, dark, horizontal surfaces, such as oil lakes (Horváth and Zeil 1996; Wildermuth 1998; Horváth et al. 1998), asphalt roads (Kriska et al. 1998), black plastic sheets (Horváth et al. 1998; Kriska et al. 2007), bodywork of black, red, and dark-colored cars (Wildermuth and Horváth 2005; Kriska et al. 2006), and black gravestones (Horváth et al. 2007), can attract different aquatic insects (Coleoptera: water beetles, Heteroptera: aquatic bugs, Plecoptera: stoneflies, Trichoptera: caddis flies, Ephemeroptera: mayflies, Odonata: dragonflies). These visually deceived insects often swarm above, land on, and oviposit onto these surfaces because they are attracted by the high and horizontal polarization of reflected light. Because these insects detect water by the horizontal polarization of water-reflected light (Schwind 1985, 1991, 1995; Horváth and Varjú 2003), they are lured to every source of horizontally polarized light, that is, they possess positive polarotaxis.

Dusk-active, aquatic insects, such as mayflies and caddis flies, for example, often swarm at buildings, which is usually explained by the so-called marker effect (Brodskiy 1973; Savolainen 1978; Reich and Downes 2003): the dark silhouette of a building against the bright

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sky can function as a conspicuous rendezvous site for swarming insects. We document here that every year in April and May, the caddis fly *Hydropsyche pellucidula* (Curtis 1834) emerges from the river Danube in Budapest (Hungary) and is attracted *en masse* to the vertical glass surfaces of buildings standing on the river bank. The individuals lured to dark vertical glass panes land, copulate, and remain on the glass for hours.

In order to understand this visual-ecological phenomenon, we observed the swarming and reproductive behavior of *H. pellucidula* at the buildings with numerous vertical glass windows and glass ornaments of the Eötvös University in Budapest. Using video polarimetry, we measured the reflection-polarization characteristics of the glass-covered walls of these buildings. We also performed choice experiments with *H. pellucidula* to study their polarotaxis.

Materials and methods

We investigated the mass swarming of *H. pellucidula* from 15 April to 15 May in 2006 and 2007. The observations were conducted almost every day from 1400 and 2100 h (local summer time = Coordinated Universal Time (UTC) + 2) at the northern and southern buildings of the Faculty of Natural Sciences of the Eötvös University in Budapest (47° 29′ N, 19° 3′ E), Hungary. Both buildings are on the bank of the river Danube 100 m apart from each other and 100 m from the river. The swarming of caddis flies was observed from both outside and inside the buildings systematically on all seven floors and at all four sides of the buildings. The tiltable glass windows of both buildings can be partly opened: a framed glass window is rotated along its lower horizontal edge by about 10°. This is of great importance in the trapping of swarming caddis flies.

Using a binocular, on 19, 20, and 22 April, as well as on 1 and 5 May of 2007, we counted the numbers of *H. pellucidula* that landed on 50 black and 50 white vertical panes of glass (each 2×2 m) of the northern building (Fig. 1b). Each counting lasted about 5 min and was repeated three times at 1730, 1800, and 1830 h (UTC+2) under clear sky, in calm and warm weather.

To study the polarotaxis of *H. pellucidula*, we performed two double-choice experiments in the laboratory. These experiments were based on the fact that after their fertilization, female caddis flies return to the water to lay their eggs. In a given experiment, 100 individuals of *H. pellucidula* were placed into an air-filled glass aquarium with dimensions 120×50×50 cm. The left (60×50 cm) and right (60×50 cm) halves of the horizontal bottom of the aquarium was covered inside by two different materials: (1) aluminium foil and shiny black plastic sheet in the first experiment and (2) matt black cloth and shiny black plastic sheet in the second one. The air in the aquarium was made vaporous enough manually by means of a common mechanical vapor emitter in such a way that plenty of tiny water droplets were sprayed onto the glass walls. After spraying, the aluminium or cloth and plastic test surfaces were placed onto the bottom of the aquarium.

Caddis flies were caught manually by a small hand net inside the buildings at partly open tiltable windows where the swarming insects became entrapped. In each experiment, 100 individuals of *H. pellucidula* were placed into the aquarium covered by a white cloth mesh and a matt light brown wooden board, which hindered the escape of the water vapor. The insects were left in the aquarium for 2 days under natural illumination conditions in the laboratory. Finally, we counted the numbers of egg batches laid by the caddis flies onto six equal rectangular zones (10×50 cm) of the test surfaces (Table 1). The number of eggs in the batches was 4–11. To compare the data pairs in Tables 1 and 2, χ^2-test was performed with the use of the computer program Statistica 6.1.

The reflection-polarization characteristics of the three horizontal test surfaces used in the choice experiments were measured by video polarimetry in the red (650±40 nm), green (550±40 nm), and blue (450±40 nm) parts of the spectrum (Horváth and Varjú, 1997). The angle of elevation of the optical axis of the video polarimeter was −35° from the horizontal, and the scene was illuminated by unpolarized white light transmitted through the white curtain of the laboratory's windows. The polarimeter's elevation was approximately equal to the Brewster angle θ_B=−36.9° and −33.7° of the water (with refractive index n=1.33) and plastic (n≈1.50)

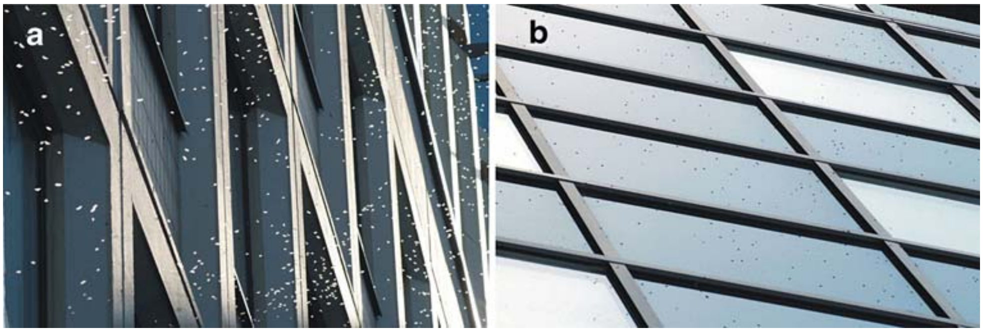

Fig. 1 **a** Mass swarming of the caddis flies *Hydropsyche pellucidula* (*white spots*) in front of the vertical glass panes of the northern building of the Eötvös University in Budapest on 1 May 2007. **b** Numerous individuals of *H. pellucidula* (*black spots*) landed on the glass panes

Table 1 Number of egg batches laid by *Hydropsyche pellucidula* onto the six zones of the horizontal (i) aluminium foil and shiny black plastic sheet, and (ii) matt black cloth and shiny black plastic sheet in the first and second double-choice laboratory experiment

Zone	First experiment		Second experiment	
	Aluminium foil	Shiny black plastic	Matt black cloth	Shiny black plastic
1	10	46	9	124
2	14	25	11	30
3	13	57	12	61
4	11	175	8	54
5	23	115	21	87
6	26	83	22	124
sum	97	501[a]	83	539[a]

[a] Data belonging to the shiny black plastic sheet, which are statistically significantly larger than the corresponding data belonging to the other two test surfaces (χ^2-test, $p<0.001$)

surface, respectively, where $\theta_B=-\arctan(1/n)$ relative to the horizon.

The reflection-polarization patterns of the vertical glass-covered walls of the northern building of the Eötvös University (Fig. 3) were measured by video polarimetry in the red, green, and blue spectral regions on 8 May 2006 at 1900 h (= UTC + 2) in the middle of the swarming period of the caddis flies lasting from 1700 h to 2100 h. During the measurement, the sky was clear, the sun was shining, the solar elevation angle was $\theta=9.4°$, the polarimeter viewed towards the solar meridian, and the elevation angle of its optical axis was + 35° from the horizontal.

Results

In Budapest, the mass-swarming of the caddis fly *H. pellucidula* begins usually in the second week of April, and lasts for about 5 weeks. In this period, adult *H. pellucidula* leave the river from about 1500 h (local summer time = UTC + 2). The first caddis fly swarms composed of some hundreds flying individuals develop after 1700 h on the river bank not farther away from the water than a few hundreds of meters. In calm weather, caddis flies swarm usually around conspicuous objects (called markers) standing immediately on the river bank while in windy weather, the swarming can take place only farther away from the river at windless places. Under rainy and cold weather conditions, we did not observe the swarming of *H. pellucidula*, which swarms only under calm and warm conditions at dusk. At first, the swarms are composed of male caddis flies, which copulate with the females flying through the swarms. The duration of the copulation is about 2–3 min. The swarming ends at about 2100 h. The fertilized females return to the river where they lay their eggs into water. Such swarming of *H. pellucidula* occurs every year along the whole Hungarian section of the river Danube inclusive the reaches in cities where the river is usually flowing among vertical or tilted concrete or rocky walls.

The dark silhouettes of trees, bushes, and buildings on the river bank against the bright sky form markers which can keep together the swarms. We observed that the vertical glass surfaces of buildings also strongly attract both sexes of *H. pellucidula* (Fig. 1). In front of a vertical glass pane of 2×2 m a swarm of 50–200 caddis flies can develop (Fig. 1a). Both females and males often land on the glass (Figs. 1b, 2a), copulate (Fig. 2b) and move randomly on it, and fly off within a few tens of seconds; this is repeated for hours. Sometimes, the individuals remain on the glass surface for hours.

The swarms often move away from a given glass pane but after 2–5 min, they return to the same or another glass surface where they spend again 5–10 min. This kind of cyclic, fluctuating swarming at glass surfaces continued every day from 1700 to 2100 h at each floor of the seven-story buildings. The slightly higher (by about 2–5°C) air temperature near the building walls heated up day-time due to direct sunshine and the places around the buildings sheltered from the wind prolonged by about 30 min the swarming of caddis flies relative to the swarming time observed on the cooler and windier river bank.

After swarming (after 2100 h), the caddis flies rested motionless on the glass surfaces and on the red bricks of the buildings. On the next day, after sunrise, we found the remaining insects resting in the shadow of the window frames and among the bricks. These individuals were motionless and, if survived, they joined to the new swarms developing again in late afternoon.

If a tiltable window, at which *H. pellucidula* swarmed, was partly open, every 3 min in average, two imagoes got

Table 2 Number (average ± standard deviation) of *Hydropsyche pellucidula* landed on black and white vertical glass panes (2 m×2 m) of the northern building of the Eötvös University in Budapest averaged for N=50 quadratic glass surfaces

Number	Date (2007)	Vertical glass surface	
		Black (N=50)	White (N=50)
1	19 April	6,6±3,5[a]	2,2±1,0
2	20 April	10,1±4,2[a]	3,0±1,3
3	22 April	17,2±5,3[a]	5,3±2,2
4	1 May	28,5±11,3[a]	5,1±2,1
5	5 May	65,2±24,6[a]	9,1±3,2

Each counting was performed at 1730, 1800, and 1830 h (= UTC + 2), and these data were summed

[a] Data belonging to the black vertical glass surfaces, which are statistically significantly larger than the corresponding data belonging to the white glass surfaces (χ^2-test, $p<0.001$)

Fig. 2 **a** Adult *H. pellucidula* landed on a pane of glass. **b** Copulating pair of *H. pellucidula* on a glass pane. **c** Numerous carcasses of *H. pellucidula* trapped by a partly open tiltable window

into the room through the aperture between the window frame and the building wall: first, these insects landed on the tilted glass pane, then began to move randomly on the glass surface, and finally got in the room. After getting in, the insects tried to fly out from the room toward the bright sky through the glass pane which, however, hindered their escape. This was a typical phototactic escape reaction. After numerous trials, the trapped insects became exhausted, dropped onto the sill, and perished due to dehydration (Fig. 2c). We did not observe any striking height distribution of the trapped caddis flies, which depends mainly on the distribution of partly open tiltable windows beside the density of swarming insects. As the sun approached, the horizon and, thus, the ambient light became darker and darker; the lights were switched on in several rooms of the buildings. The lights of these rooms might also lure the swarming caddis flies by simple phototaxis. If the tiltable windows of the lightened up rooms were partly open, these swarming insects may have been trapped similarly as described above.

Figure 3 shows examples for the reflection-polarization patterns of a wall of the building, at the vertical glass surfaces of which *H. pellucidula* swarmed. In the colored picture, we can see that the wall is patchy because it is covered by different glass surfaces: beside the transparent glass windows, there are also light gray, dark gray, and black, non-transparent vertical glass surfaces. The latter glass surfaces function simply as an architectural decoration. In some of the transparent glass windows, the white blinds are dropped, which results in a brighter appearance of the windows. If the blinds are raised, the windows would appear darker due to the small amount of light coming from the dark rooms. Usually, some of the tiltable windows are partly open. The amount of light reflected from such tilted glass panes is different from that reflected from the vertical glass surface of closed windows.

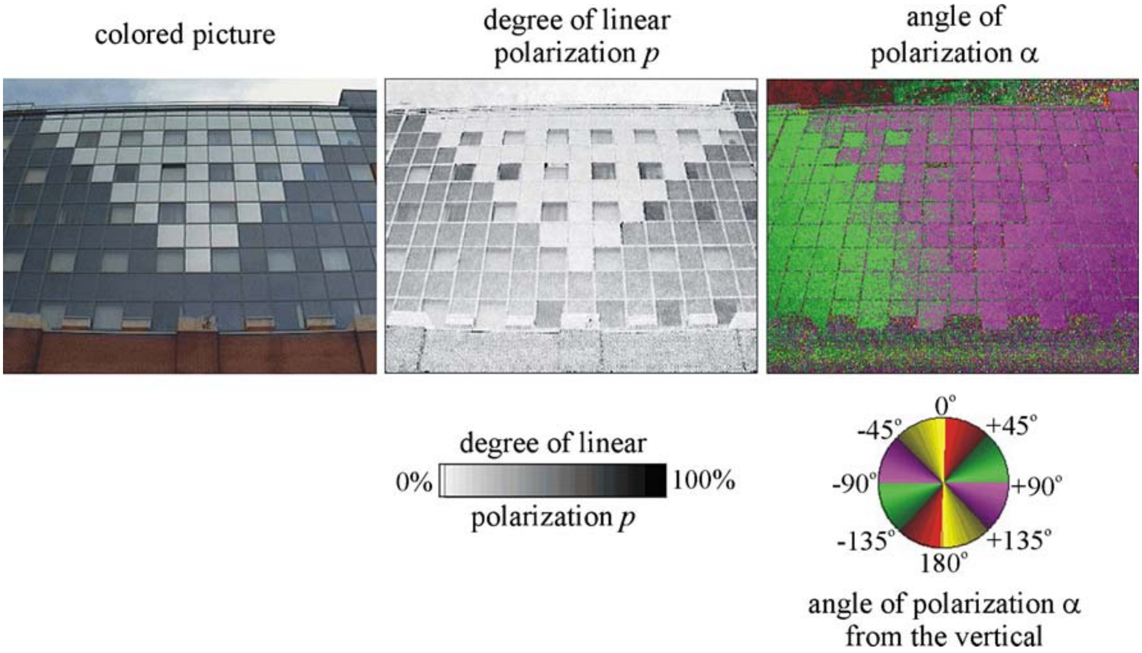

Fig. 3 *Colored picture* and patterns of the *degree of linear polarization p* and *angle of polarization* α (*from the vertical*) of the northern building of the Eötvös University measured by video polarimetry in the *green part of the spectrum*. Quite similar patterns were obtained in the *red* and *blue spectral ranges*

According to our polarimetric measurements, the darker a glass surface is, the higher the degree of linear polarization p of reflected light. Because these glass surfaces are colorless (from white through gray to black), p of light reflected from them is practically independent of the wavelength. The light reflected from the red bricks of the building walls is also partially polarized, the p of which is the lowest in the red part of the spectrum and the highest in the blue spectral range. All these correspond to the rule of Umow (1905). The p-pattern of the walls is also patchy because p of reflected light depends both on the brightness and the tiltness of the reflecting surface (Fig. 3).

The pattern of the angle of polarization α of a given wall of the buildings depends on the direction of view relative to the solar meridian. However, during the swarming of caddis flies, the direction of polarization of reflected light is always horizontal for the wall facing toward the antisolar meridian, if it is viewed from a direction parallel to the solar meridian (Fig. 3). Note that the caddis flies emerging from the river Danube see the buildings always from this direction.

Table 1 shows the numbers of egg batches laid by *H. pellucidula* onto the horizontal aluminium foil, matt black cloth, and shiny black plastic sheet covering the bottom of the aquarium in the first and second double-choice laboratory experiments. It is clear that egg-laying *H. pellucidula* preferred the strongly and horizontally polarizing shiny black plastic sheet against the weakly and/or non-horizontally polarizing other two test surfaces: 5.2 and 6.5 times more egg batches were laid onto the black plastic than onto the aluminium foil and the matt black cloth, which are significantly different statistically (χ^2-test, $p<0.001$).

We measured the reflection-polarization characteristics of all three horizontal test surfaces used in these choice experiments. These characteristics were practically the same for all three (red, green, and blue) spectral ranges because the test surfaces were colorless and the unpolarized illumination was white; p of light reflected from the shiny black plastic sheet was high ($p=70\pm25\%$, average ± standard deviation) and the direction of polarization was horizontal. The light reflected from the aluminium foil was weakly polarized ($p_{\text{aluminium}}=30\%\pm15\%$) and its direction of polarization was not always horizontal (oblique or vertical). At normal incidence, the aluminium foil reflected about 20 and 25 times much amount of light as the shiny black plastic sheet and the matt black cloth, respectively. The light reflected from the matt black cloth was practically unpolarized ($p=3\pm3\%$).

The vertical walls of the northern building are partly covered by black and white glass surfaces as an ornamentation (Fig. 3). Caddis flies swarmed at and landed on both of these black and white glass panes (Figs. 1 and 2). Actually, this offered us a third double-choice experiment in the field: prior to landing, every flying caddis fly had to choose between a black and a white glass. According to Table 2, the black vertical glass surfaces attracted, in average, 3,0–7,2 times more caddis flies than the white ones. These differences are again statistically significant (χ^2-test, $p<0.001$). According to the rule of Umow (1905), the darker a reflector is, the higher the degree of linear polarization p of reflected light. This is the reason for our imaging polarimetric finding that p of reflected light was much higher for the black vertical glass surfaces ($56\% \leq p \leq 95\%$) than that for the white ones ($12\% \leq p \leq 25\%$; Fig. 3); p was practically independent of the wavelength, but it strongly depended on the direction of reflection.

Discussion

In our first and second choice experiments, the attraction of the highly and horizontally polarizing black plastic sheet to egg-laying caddis flies was statistically significantly larger than that of the weakly and not always horizontally polarizing other two test surfaces (Table 1). In the reaction of these caddis flies, the role of positive or negative phototaxis can be excluded; otherwise, they should have strongly been attracted also to the bright aluminium foil or to the dark matt black cloth, respectively. From these, we conclude that ovipositing *H. pellucidula* are attracted to highly and horizontally polarized light; that is, they possess positive polarotaxis. In our third choice experiment, the highly polarizing vertical black glass surfaces were statistically significantly more attractive to both male and female *H. pellucidula* than the weakly polarizing white ones (Table 2). This supports further our main conclusion that *H. pellucidula* has positive polarotaxis. Note that male caddis flies should also be polarotactic because they also must find water, where the females occur (Horváth and Varjú 2003). Hence, these insects find water by means of the horizontally polarized water-reflected light, like aquatic insects in general (Schwind 1991 1995; Horváth and Varjú 2003; Bernáth et al. 2004; Csabai et al. 2006).

It is still unknown which parts of the eye in *H. pellucidula* are polarization sensitive. The morphological and electrophysiological study of this could be an interesting task of future research. However, according to our laboratory experiments, we know that ovipositing female *H. pellucidula* have positive polarotaxis, if the ventral region of their eyes is stimulated by highly and horizontally polarized light. If the eye of *H. pellucidula* had only a ventral polarization-sensitive eye region, like the backswimmer *Notonecta glauca* (Schwind 1985), for example, then a flying *H. pellucidula* could be attracted by polarized light to a vertical glass surface only, if the insect approaches the glass at an appropriately large (a few meters) height from the ground. Only in this case could the horizontally polarized glass-reflected light stimulate the ventral eye region; then, the light originating from the ground is reflected from the vertical glass surface toward the eyes of the flying insect. This glass-reflected “ground light” is always nearly horizontally polarized because the direction of reflection is then always approximately vertical. We observed that the height of the swarms of *H. pellucidula* at the buildings was always larger than a few meters.

Caddis flies usually move away from their emergence sites only at distances from which they can see the horizontally polarized water-reflected light. However, *H. pellucidula* swarmed also on those sides of the investigated buildings, from which the river Danube was not visible. The reason for this may partly be that all glass surfaces of the buildings can reflect horizontally polarized light and, thus, can be attractive to polarotactic caddis flies. Because the caddis flies swarming at the river side of the building still see the river surface, there is a chance that some of the fertilized females return to the river to oviposit. On the other hand, because the caddis flies swarming at the opposite side of the buildings do not see the river, they remain near the water-imitating, horizontally polarizing glass surfaces, where they necessarily dry out or became trapped by the partly open tiltable windows and perish together with their eggs (Fig. 2c).

The two buildings studied by us, similarly to many other modern buildings, possess such an unfavorable air-conditioning system which, according to the original intention of the designers, makes the airing superfluous through fully-open windows. Thus, the majority of the windows in these buildings are tiltable, which can be only partly open by rotating around their lower horizontal edge by about 10°, rather than entirely open by rotation around a vertical axis as the conventional windows. Many of these tiltable windows are partly open the whole day, inclusive of evening and night, also in April and May—months when the main swarming period of many polarotactic aquatic insect species take place, the majority of which fly near dusk (Bernáth et al. 2004; Csabai et al. 2006). We propose that these dusk-active water insects could be attracted to these buildings (1) by their dark silhouettes against the bright sky (marker effect), then (2) by means of positive polarotaxis elicited by the horizontally polarized light reflected from the glass surfaces, then (3) by means of positive phototaxis elicited by the light emitted from the illuminated rooms after sunset, and finally, (4) the partly open tiltable windows trap the lured insects getting in the rooms.

We observed this trapping mechanism only in the case of the widespread and mass-swarming caddis flies *H. pellucidula* (Malicky 2005) at buildings on the bank of Danube in Budapest. In the Budapest section of Danube, there is no other mass-swarming caddis fly species. On the other hand, in the vicinity of the Eötvös University, aquatic beetles, bugs, dragonflies and mayflies occur only sporadically; thus, we could not observe their possible attraction to the glass buildings. However, actually, all such glass buildings could be ecological traps (Schlaepfer et al. 2002) for all polarotactic aquatic insects, which perish together with their eggs after being trapped. Tall buildings that are attractive to polarotactic aquatic insects, because of their polarizing properties, could become ‘meeting points’ of these insects, bringing males and females more easily together in such ‘focal areas’ rather than near some scattered natural meeting places. This phenomenon could be advantageous to these insects but only in that case if they do not oviposit onto the glass surfaces and/or are not trapped by the partly open windows.

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