DOI: 10.61782/fa.2025.0139

FORUM ACUSTICUM
EURONOISE 2025

ANTHROPOGENIC NOISE AND ARTIFICIAL LIGHT AT NIGHT: ADDITIVE AND INTERACTIVE EFFECTS ON ACTIVITY LEVEL AND SPATIAL BEHAVIOUR

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ABSTRACT

Visual and auditory sensory capacities play an important role in the animal kingdom in communication and orientation. For most animals, sound and light are most prominent in relatively long-range signaling and in gathering information about their local and more distant environments. Natural conditions for each modality have therefore continuous impact on general activity level and on spatial decisions to get closer, go further away, or stay put. Insight into these fundamental processes is critical to understand the potential effects of pollution from anthropogenic noise throughout the day and artificial light at night. The impact of sound and light on animal responsiveness roughly follows the same principles and the effects may add up or show interactive effects. We will address fundamental and applied insights into the potential effects of noise and light pollution, by themselves and in concert, and we present an early case study on Lake Victoria cichlids with experimental exposure to elevated intensity levels of both sound and light. We conclude with addressing the specific conditions of migratory fish, and we argue that it is critical to study them for potentially negative consequences of short- and long-term effects of anthropogenic noise and artificial light at night.

Keywords: *multi-modality, phonotaxis, phototaxis, skyglow, soundscape*

1. INTRODUCTION

Sound and light play an important role in the life of animals. Natural sound and light background intensities and spectra determine general activity levels and affect circadian or seasonal rhythms. Specific sound and light sources can also influence spatial decisions: drawing animals closer (attraction) or driving them away (deterrence). This is also referred to as positive and negative phonotaxis and phototaxis [1,2]. For many species, sound and light are the principal modalities used to communicate with conspecifics and to extract information from their environment. Sounds are generated in a variety of ways, propagate through the environment, dependent on habitat- and condition specific scattering and absorption, after which they have communicative potential within the audible range of conspecifics. Behavioural displays and colouration only become visible in the presence of light and when reflected light meets the eye. Objects in the habitat and context will also play a role in detection probability, next to visual attention. Auditory and visual stimuli are often used in concert for communication, and also typically co-occur as environmental cues. Their perceptual prominence varies as with communicative signals with the environmental conditions, behavioural context, and focus (hearing is continuous and omnidirectional, watching is restricted to a particular angular focus and field of vision. In the Anthropocene, both light and noise pollution have altered the world and thereby also the

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multi-modal perception of communicative signals and environmental cues.

1.1 Sounds of sexual selection and survival

Natural soundscapes include all that is audible in the environment for an individual animal in a particular habitat at a specific time of day [3,4]. The onset of vocalizations of conspecifics or heterospecifics in the morning may wake up animals and stimulate them to do the same or start other activities, such as foraging or nest-building (Figure 1). Also gradual fluctuations over the day in audible presence of local animal communities may affect vocal and other activity levels. Vocal activities are fluctuating seasonally, driven by hormonal variation over the year, likely stimulated by day length and temperature. The acute effect of natural soundscapes per day may therefore also contribute to longer-term, stimulating effects on physiological and behavioural cycles related to seasonal migration and reproduction. The ability to respond and participate in vocal interactions can for example be critical for reproductive development and mate choice in birds and thereby affect breeding success. Natural soundscapes may also suppress activities when they indicate potential danger by the presence or arrival of a predator. Responsiveness in slowing down activity can then directly translate into survival. Conversely, the resurgence of natural level and composition of local soundscapes may signal the apparent release of danger and trigger revival of halted activities. Abiotic sounds of rain or wind can also affect vocal or other activity levels, likely related to the masking effect on their own vocalizations or on audibility of predator risk, or through learned association with rain or wind, which may be unfavourable to many activities.

1.2 Ambient light by day and night

Light intensity as perceived by animals depends on their visual abilities and the species-specific sensitivity for parts of the light spectrum. The response to light intensity in terms of general activity level is determined by their nocturnal, crepuscular, or diurnal life style (Figure 1), which varies among and within species [5,6]. The length of daylight varies by season and latitude and tunes the biological clock of animals in such a way that their activity levels are optimally timed to ecological opportunities related to feeding and breeding, and to risks of predation and disease. This means that light conditions not only have acute effects, but also influence longer-term physiological and behavioural cycles, such as migratory and reproductive seasons. Acute effects of natural daylight could be regarded as stimulating when triggering activity of diurnal animals, but also as suppressing when making nocturnal animals seek shelter. Twilight and moonlight have a different spectrum and intensity and may also be stimulating or suppressing, depending on species and context. Nocturnal and crepuscular animals typically have special visual adaptations to see at low light intensities (scotopic vision), usually correlated to declines in colour vision or shifts in spectral sensitivities towards colour ranges that are relevant at the dim hours of the day.

1.3 Anthropogenic noise and artificial light at night

Noisy conditions due to human activities [7,8] and artificially lit up nights [9,10] typically disturb or distract animals, generally leading to lower activity levels of whatever they would have done at the time and place (Figure 1). Anthropogenic noise is typically louder, more repetitive, and lower in frequency, than natural sounds. Any time of day, such noisy conditions may elicit fear, stress, or anxiety, making animals to reduce activities that would be risky under the acoustic conditions of perceived threat. Noisy conditions may also just distract, as animals of various taxa have been shown to be unable to avoid processing audible sound, and they thereby lower activity levels of behaviours that require attention for appropriate performance. Finally, masking may yield decreased activity levels through lower stimulating effects of natural soundscapes or reduced opportunities for auditory predator scanning. Lower vocal activity levels may also be the result of lowered auditory feedback from hearing less of their own sounds or of vocal responses from conspecifics. Interestingly, there are also birds and frogs that are vocally triggered by anthropogenic sound events and many species that elevate their vocal intensity and sound production rate in response to more continuously elevated noise levels due to human activities.

Artificial light at night takes away the safety of dim and dark conditions that allow many prey animals to room around with lowered predation rates. Despite intensity typically being much less than natural day time light levels, direct light from lamps, and even indirect light reflected from clouds and air of high humidity (skyglow), usually outcompetes by far any natural light at night from moon or stars. Even though not all diurnal predators become active at night at lit up places, many nocturnal prey species may be less active under artificially elevated conditions and spend less time on critical activities such as foraging, exploring, socializing, and courting. Interestingly, artificial light at night may also trigger or stimulate activity levels. Birdsong is known to be starting earlier and to end later during the day at territories lit up by artificial light. Predatory fish and birds like herons or grebes may go hunting for fish at times of day that would naturally be too dark to see their prey.

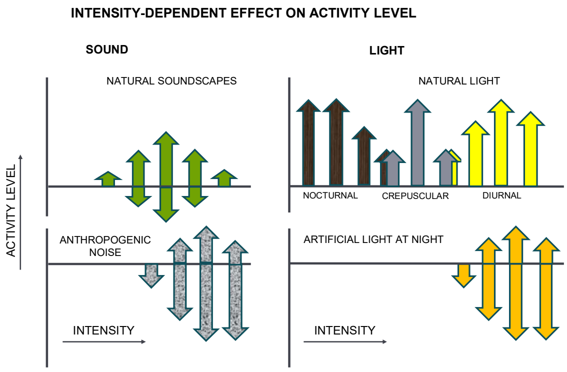

Figure 1: Sound and light conditions can affect general activity level. Soundscapes of conspecific and heterospecific sounds indicating safe conditions for foraging or social activities may elevate activity level in a parabolic way from modest to familiar to extreme sound levels. Natural light levels may stimulate activity depending on whether species are nocturnal, crepuscular, or diurnal. Anthropogenic noise and artificial light at night can also trigger or stimulate activity of animals that are usually not or less active at night, but more often suppress activity of nocturnal and crepuscular species with increasing intensity.

2. CICHLID CASE STUDY

A study with Lake Victoria cichlids (*Pundamilia nyererei*) at Leiden University in August and September 2009, provides a nice example of suppressing effects of sound and light on activity level [11]. Christina May exposed solitary males to noisy or ambient quiet conditions, in bright or dark conditions, and scored their swimming activity and style. After that, she added a female and quantified the courtship behaviour and male calls per pair under the four combinations of sound and light exposure treatments. Earlier studies in this species had shown that both noisy conditions [12] and light intensity and spectrum [13] affect swimming patterns and spatial preferences respectively, likely through familiarity, stress, or anxiety related tendencies to engage in explorative activity. Furthermore, both male sound production [14] and male colouration during behavioural displays [15] have been shown to play a role in communication among male cichlids and in female mate choice.

2.1 Cichlid methodology

We used 40 unique pairs of cichlids from our Leiden stock at the time. These fish were three-year-old, lab-raised individuals [c.f. 14]. All recordings and behavioural observations were made in the same experimental tank (300 x 100 x 100 cm, water level at 90 cm, swimming area restricted to 200 cm, away from both ends). Housing conditions and all experimental procedures were in accordance with guidelines of the Association for the Study of Animal Behaviour and licensed by approval from the ethical committee on animal experimentation of Leiden University (licence number: UDEC 08055). Male and female cichlids within a test pair always came from different stock tanks and were unfamiliar to each other. Relatively large or small males were paired with relatively large or small females respectively, and randomly assigned to sound and light conditions. At the end of the test, fish were transferred back to the stock tank, where they resumed normal activities, and were kept alive as breeding stock.

During the experimental exposure, cichlids experience ambient sound levels at 116 dB re 1 uPa, from the ambient building conditions in the aquarium facilities at the Gorlaeus building of Leiden University. We used an ING 32mV amplifier with an MR23333-000 waterproof speaker (Knowles Electronics, Itasca, IL), in the center of the tank, 10 cm below the water surface, connected to a desktop computer for playing back sound underwater. The speaker was in the water and turned on, but not playing back any sound for the ambient sound treatment. During elevated noise conditions, we played back white noise between 500 and 2000 Hz to generate sound levels of 119 re 1 uPa, which reflects possible conditions for nearby human machinery or boat presence in natural waters. Cichlid calls center around 500 Hz, and they readily respond to playback of calls and white noise of the same frequency range and temporal pattern [14,16]. This made it likely that they would also hear the artificially elevated noise levels in the current set-up, while we would not miss any courtship calls due to masking. Bright and dark light levels in the aquarium were adjusted to 19,800 and 770 Lux, respectively (measured with a light meter and nAmp converted to Lux). The measurements and light levels corresponded with samples taken at Lake Victoria close to the surface and at 6 meters depth (~21,000 and 325 Lux) respectively (Frans Witte, unpublished data).

For the experiment, male and female were introduced in the 200 cm tank arena, on either side of an opaque divider, with a sandy bottom and a three-rock shelter on the male side. After an hour of acclimatization, the male swimming behaviour was observed and scored for 15 min, using JWatcher V6.1. After another two hours, the opaque divider between male and female was removed and we observed courtship interactions for 15 min and recorded any male calls, using an HTI 96-min hydrophone (High-Tech, Inc, Gulfport, MS), with a 20-dB amplifier, and a digital recorder (Marantz PMD 660, WAV-format, 44.1-kHz sampling rate). We analyzed our data with JMP (version 8.0) and R (version 2.10.1) statistical software. Shapiro-Wilk tests revealed that our data were not normally distributed and we applied general linear models, using a Gaussian distribution and identity link for continuous response variables (swimming and window swimming) and a Poisson distribution and log identity for count data (courtship quivers and calls). Male size caused variability, but did not affect treatment dependent patterns.

2.2 Cichlid results

General swimming behaviour of solitary males appeared to go down but was not significantly affected by sound treatment (F = 0.09, p = 0.77). In contrast, during the dark conditions the male cichlids were significantly more away from their rock shelter and swam significantly more than during the bright conditions (F = 23.39, $p < 0.0001$, see Figure 2). In the time swimming, they also exhibited a stereotypical window-swimming behaviour, with their noses against the glass, going up and down and left and right, usually regarded as an indication of discomfort. Of the time swimming, they swam significantly more in this mode of window swimming in noisy compared to ambient quiet conditions (F = 4.30, $p < 0.05$), which was not affected by light treatment (F = 0.02, p = 0.88).

Courtship behaviour of the pairs of cichlids was affect by both sound and light treatments (Figure 2). The noisy treatment yielded significantly less lateral quiver displays than the quiet treatment (F = 5.02, $p < 0.05$) and the bright significantly less than the dark treatment (F = 5.20, $p < 0.05$). As, two out of the ten pairs for the quiet and dark condition were highly active, with only modest activity for the 30 pairs in the other conditions, there also was a significant interaction (F = 6.38, $p < 0.02$). Vocal activity of the males was especially low for the bright conditions, and not very different for the sound treatments in the dark conditions, which yielded a non-significant effect of sound on call rate (F = 1.66, p = 0.20) and a significant impact of light on call rate (F = 17.10, $p < 0.0001$), and no interaction effect.

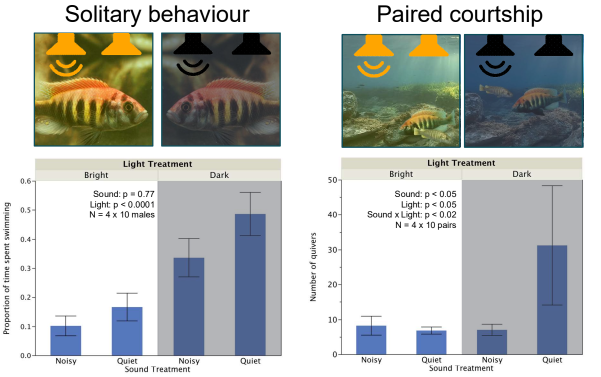

Figure 2: Multi-modal exposure experiment with *Pundamilia nyererei* cichlids. Male cichlids were exposed to playback-induced noisy conditions or ambient control conditions (2 x 2 design) and to bright or dark light conditions. Both sound and light reduced activity levels in a way: cichlids swam significantly less under bright light than dark conditions (left graph), and were involved more in window swimming under noisy than quiet conditions. When a female was introduced, modest levels of courtship where observed, except for two out of the ten pairs in the dark and quiet conditions, which were very active with quivers, and hence the significant effect of both light and sound and a significant interaction (right graph). Courtship call rate was also significantly reduced by light, not by sound.

3. EFFECTS ON SPATIAL DECISIONS

3.1 Looming and luring sound conditions

Besides the effects on activity level, anthropogenic noise and artificial light at night can also affect spatial decisions. Many studies investigated the potentially negative effects of anthropogenic noise on aquatic animals and deterrence is probably one of the most reported effects. Noise exposure level is often varying in amplitude, as vessels are for example moving, and approaching vessels may acoustically suggest a looming threat. Driving away in fear is also the focus in acoustic deterrent studies, in which responsiveness to human-made sounds is investigated as application for herding marine mammals away from fishing nets [17] or guiding fishes away from harmful pumping stations [18]. Variation in acoustic features may determine effect sizes, but typically deterrent capacity is assumed to be positively related to sound intensity (Figure 3).

However, anthropogenic sounds can also be audible and not drive animals away and even attract them out of curiosity or after experience with positive rewards when human activity underwater yields feeding opportunities. Although even loud deterrent devices like pingers have been shown to be successful in their targets at first and become a dinner bell after dolphins find out that they are associated with full nets of fish, amplitude levels of attractive sounds are likely to be relatively low amplitude (Figure 3).

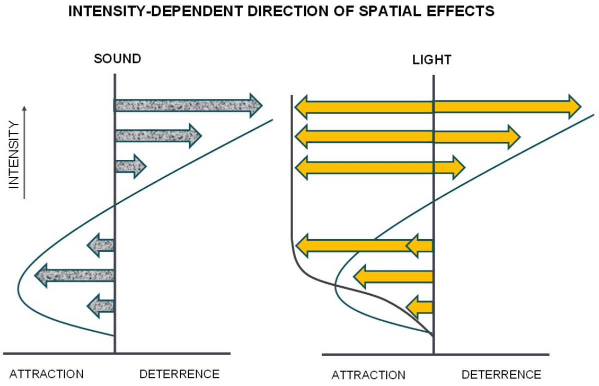

Figure 3: Generalized and schematic illustration of spatial responsiveness to sound and light relative to intensity. At low intensity, animals may just detect sound or light and become interested and be drawn towards the source. At higher intensities, this phonotactic or phototactic behaviour may get stronger, up to an optimum level at which the attractive power starts to decline again. Sound and light may also become deterrent and get stronger towards more extreme intensities. For some animal groups, intense light seems not to become aversive and phototaxis can even become stronger, persistent, maladaptive, and often fatal.

3.2 Fatal attraction: blinded by the light

The spatial effects of artificial light at night can have a similar pattern as anthropogenic noise (Figure 3). Animals with nocturnal habits or living in dark habitats typically avoid bright areas and move away from light sources. The higher the light intensity, the higher the probability of spatial deterrence. However, also at lower intensities of light, animals may be drawn towards the source out of curiosity and the explorative nature of the species or caused by positive experience with food-associated light sources. Actually, there are many examples, in contrast to sound in which the attractive effect of light does not fade with intensity. Moths and many nocturnal insects are attracted to bright lamps at night. Also migratory birds are known to be attracted to brightly lit oil platforms at sea [19] or exceptional beacons of light, such as the Tribute in light, an annual art installation at the Twin tower memorial site. The insects and birds seem to blinded by the light or at least loose the capacity to escape the light source site as long as the light is on. Another fatal attraction is found in marine turtles, where juvenile animals, just out of the egg, crawl on the beach into the wrong direction: towards lamps of coastal roads or buildings, away from the ocean which they used to find by going for the bright side with most open sky [20].

3.3 Multimodality

Given that most animals have perceptual abilities for both sound and light, they are likely to be affected by both all the time [21]. Responsiveness to playback of conspecific song may yield a different response strength depending on amplitude and other acoustic features, but may also vary between bright and dark conditions. Similarly, the response strength to a visual display of a fish during particular light conditions may be modified by ambient sound levels from nearby conspecific or heterospecific vocalizations or by the rustling of leaves in the wind. Consequently, also the effects of noisy conditions and artificial light at night will depend on multimodality. Noise and light pollution may co-occur at night, such as with passing cars or brightly lit highways or industrial areas, but each may also occur independently of each other. Noise and light pollution may have unimodal, cross-modal, and multimodal effects [21]. Multimodal effects may be in the same or opposite direction [22], with respect to stimulation or suppression of activity level and with respect to attraction or deterrence (Figure 4).

3.4 Additive and interactive effects

The co-occurrence of both anthropogenic noise and artificial light at night may yield additive effects, where the combined effect is equal to the sum of each separately (Figure 4). If the effect is in the same direction, they add up, if they are in opposite direction, they get subtracted. The effect of sound and light exposure on swimming activity in the cichlid case study suggested such an additive effect in the suppression of activity. The effect of courtship quivers seemed to be more dramatic and either of the stressors seemed to have a similar suppressive impact as the two together, although this may also be due to a bottom effect. The pattern yielded a significant interaction, as the absence of noisy conditions was only yielding high activity levels in dark and not in bright conditions. More interactions are possible, for which there are no or limited examples available at the moment, where there may be antagonism and synergism [22], leading to variable patterns for effects in the same and different direction (Figure 4).

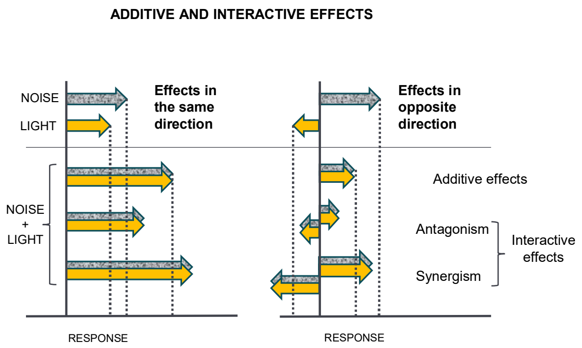

Figure 4: Spatial responsiveness to light and sound can involve attraction and deterrence, depending on the intensity (figure 2), and co-occurrence of both modalities can thus result in responsiveness into the same (left panel) or opposite direction (right panel). The combined effects of both can be additive and yield the sum or subtraction of both of the directional responsiveness. Sound and light can also interact and yield antagonistic or synergistic effects that are more complex (after [22]).

3.5 Particle motion of sound and polarized light

Sound and light can be characterized by intensity and spectrum, but there are additional features with similar aspects and consequences for animal species that can perceive these. For most aquatic invertebrates and fish, sound is perceived through the particle motion aspect of sound [23,24], which makes sound pressure level measurements less reliable in terms of exposure conditions, especially when close to boundaries with air, rock, or bottom. The sensitivity to particle motion can be extended with pressure sensitivity in case there is a gas-filled cavity such as a swim bladder. In both cases, the animals perceive directionality through the particle motion. Relative particle motion levels of a sound from a source at a particular distance and angle are dependent on ambient noise from just the same direction. Signal-to-noise ratios are therefore favorable compared to sound pressure of an unidirectionally arriving signal and omnidirectionally accumulated ambient noise. There is also a special role for polarized light for some species groups: the oscillation of the electric field vector of light can be detected by many invertebrates. Insects can for example use the polarization of light to detect water, improve visual contrast, undermine camouflage, navigate through landscapes, and even to signal during mating [25]. Many animals that also exploit the direction of light polarization as a source of information may be detrimentally affected by light that has been polarized through interaction with human-made objects, such as reflective windows at large office buildings, car window screens, or specific parts of wasted bottles [26].

4. THE CASE FOR MIGRATORY FISHES

In this final section, we would like to draw attention to migratory fish. Migratory fish provide an interesting case for studying the effect of both sounds and light in terms of activity level and spatial decisions, as done in the context of the EU Horizon-project AquaPLAN. We lack fundamental insights into the role of natural soundscapes and natural light during day and night. Furthermore, the expansion of noise and light pollution in and around aquatic habitats is spreading worldwide and may warrant the label acoustic climate change [7]. Freshwater ecosystems are among the most vulnerable in the world and the protection of especially migratory fish is a major challenge, because their decline is often caused by multiple stressors. These stressors include blockage of migratory routes, overfishing of populations, water quality changes and habitat deterioration [27].

4.1 Noisy conditions on migration

On top of the many recognized stressors, both noise and light pollution may add significant problems. The habitat of migratory fishes has been increasingly affected by anthropogenic noise worldwide, especially due to an increase in the number and size of shipping vessels [28]. Natural soundscapes are increasingly recognized as an important ecological feature of critical importance to animals [3,29]. Sounds audible to freshwater fish may include sounds of mammals, fish, frogs, and aquatic invertebrates, gas bubbles produced by aquatic plants and decomposing bacteria, but also physical disturbance of the substrate or water surface by animal or water currents and wind [28]. However, high levels of shipping and recreational activity may render the acoustic cues about the river environment inaudible and this may also be true when rivers flow through noisy urban areas. Migratory fish are therefore constantly challenged acoustically, as spatial details, temporal dynamics, and directionality of natural auditory cues can be masked and become inaccessible.

4.2 Light on short- and long-term effects

Also light pollution along rivers and coastal areas has spread worldwide. Natural light cycles are increasingly disrupted by artificial light pollution [30]. Currently, ~80% of the global population resides under light-polluted skies, and artificial sky brightness continues to rise. Artificial light at night impacts freshwater ecosystems both directly, via illuminated infrastructure like bridges and vessels, and indirectly through skyglow caused by atmospheric light scattering [31], and might disrupt specifically light-dependent biological processes such as migration. In species such as Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*), artificial light at night has already been linked to various detrimental short-term and long-term effects, such as increased predation, disorientation, and delayed migration timing [32]. The alignment with the biological clock is likely to be especially vital during migration, but more studies are needed to shed a better light on problems and potential solutions.

5. CONCLUSIONS

Sound and light play an important role in the live of all animals and especially migratory fish. Sound and light conditions affect general activity levels and may influence spatial decisions. Noise and light pollution can detrimentally affect these natural processes and undermine adaptive responsiveness to the natural environment. More studies are required to gain insight into the fundamental nature of positive and negative phono- and phototaxis, both to natural and artificial conditions. Studies in captivity such as in the cichlid case study may be suitable to explore additive and interactive effects and migratory fish may provide a suitable and important model system to investigate responsiveness to experimental exposure to anthropogenic noise and artificial light at night in their natural habitat.

6. ACKNOWLEDGMENTS

HS received funding through AquaPLAN and SATURN; LD is PhD-student for AquaPLAN; DC is PhD-student for BioClock; KtV is PhD-student for SATURN. CT received funding through BioClock. AquaPLAN and SATURN are funded by the European Union, Horizon Europe, Research and Innovation Programme: grant No.101135471 (AquaPLAN) and No. 101006443 (SATURN). BioClock is funded by the Dutch Research Council (NWO) in the framework of the National Research Agenda (NWA): grant No. NWA.1292.19.077.

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