Microclimate and the effect on incubation behaviour across different timescales in Pied Flycatchers

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The author declares that

1) this work is their own and
2) they adhered to The Netherlands Code of Conduct for Academic Practice

Abstract

Incubation behaviour in birds is influenced by various environmental, temporal and breeding parameters, yet the relevant timescale for these factors remains unclear. This study investigates the incubation behaviour of Pied Flycatcher (*Ficedula hypoleuca*) across multiple timescales (4 minutes, hourly and daily), exploring the relationship with microclimatic conditions, clutch size, lay date, incubation progression and hour of the active day. We monitored nest attentiveness, off-bout number and duration and microclimatic conditions, such as temperature and humidity, combined as the biologically relevant heat index, and UV index. We developed sensor-coupled microcontrollers (Arduino UNO) to measure the microclimate at the nestbox (n = 22).

Our results show that different timescales reveal distinct behavioural responses to the microclimatic conditions. Attentiveness increased with heat index across all scales, with decreasing number and duration of off-bouts on warmer days. The hourly scale provided the most extensive insights into behavioural responses to heat and UV index, while the 4-minute scale showed fine-scale, but less significant, variation in response to microclimatic fluctuations. Interestingly, no significant effect of clutch size or lay date on incubation behaviour was observed, and attentiveness decreased slightly as incubation progressed- contrary to our expectations.

We conclude that different components of incubation behaviour are best captured at varying timescales, with the hourly scale as a key temporal window for the influence of microclimatic conditions. Future research could apply a sliding window approach to further approach the optimal timescale for predicting incubation behaviour.

Introduction

Breeding is costly and poses multiple trade-offs for birds. Decisions on breeding timing, clutch size, and incubation behaviours are associated with food availability (García-Navas & Sanz, 2011; Martin, 1987; Ruffino et al., 2014), predation avoidance (Higgott et al., 2020; Martin & Ghalambor, 1999; Matysioková & Remeš, 2018), embryonic development (Conway, 2000; Cooper & Voss, 2013), and self-maintenance (Amininasab et al., 2016; Cooper & Voss, 2013; Walters et al., 2016). Breeding is especially costly in uniparental incubators, such as the Pied Flycatcher *(Ficedula hypoleuca*), during which females must trade off reproductive investment and self-maintenance, for instance incubating and foraging. Reproduction investment has future fitness effects on both the parents and offspring (Visser & Lessells, 2001). With increasing clutch size, energetic demands of incubation are increased (Haftorn & Reinertsen, 1985).

During incubation, embryonic development and, thus, hatchability are influenced by variability in temperature and humidity (Conway, 2000; Diez-Méndez et al., 2021; Diez-Méndez et al., 2021; Higgott et al., 2020; van der Pol et al., 2013). As a result, environmental conditions play an important role in decisions on breeding timing and incubation strategy. Higher ambient temperatures during the active day (civil dawn to civil dusk) allow females to spend more time off the nest as egg-cooling is reduced (Diez-Méndez et al., 2021). But, ambient temperature across different timescales also affects breeding decisions. For example, the temperature of early spring is known to affect the lay date in Great Tits, with warm early-spring temperatures advancing the lay date by a few days (Schaper et al., 2012). Also, the start of incubation is known to be delayed when Great Tits experience colder temperatures during the laying period (Diez-Méndez et al., 2021). Incubation timing can be used as an adaptive measure, by delaying incubation initiation or starting partial incubation before clutch completion to shorten total incubation time (Diez-Méndez et al., 2021; Podlas & Richner, 2013; Simmonds et al., 2017; Wang & Beissinger, 2011), to account for unexpected changes in climatic conditions or mistiming to match the peak food abundance. Furthermore, the number of eggs in a clutch is reduced in colder regions, but egg volume is increased, likely to minimize individual egg cooling and ensure offspring survival. With advancing embryonic development, egg cooling rates increase and the eggs are more sensitive to large temperature fluctuations (Cooper & Voss, 2013). Females are known to increase nest attentiveness through the incubation period, as eggs develop till hatching (Álvarez & Barba, 2014). These cases highlight the pivotal role environmental conditions play in decisions in breeding and incubation behaviour(al responses), posing a parent-offspring trade-off, across different timescales.

Recent studies have emphasized the importance of considering microclimate in relation to life-history trade-offs (Bramer et al., 2018; Kemppinen et al., 2024; Kim et al., 2022; Mueller et al., 2019). Microclimate refers to the environmental conditions on a local scale, relevant to the perception of the species of interest (Bramer et al., 2018; Kemppinen et al., 2024; Potter et al., 2013). Potter et al. (2013) showed in their meta-analysis that studies frequently use environmental conditions at a scale 10 000-fold larger than their subject organisms, illustrating the nature of the mismatch between the scales at which organisms sense and respond to their environments and the scale on which environmental covariates are derived (Levin, 1992). The microclimate can differ substantially from the macroclimate in an area (Bramer et al., 2018). Microclimates are often strongly heterogeneous and can provide suitable habitats in a generally unsuitable macroclimate and vice versa (Kemppinen et al., 2024). Individuals within the same season may experience different microclimatic conditions, depending on their reproductive timing and local variation in vegetation, orientation and topology (Kemppinen et al., 2024; Kim et al., 2022; Shutt et al., 2022; Williams et al., 2023).

While microclimatic conditions are known to influence incubation behaviour, likely at the level of an individuals' local environmental perception, the data is often collected at a much coarser level (Kemppinen et al., 2024; Potter et al., 2013). For example, in studies that make use of standardised weather station data (i.e. collected through national weather monitoring programs), the temperature or precipitation at a specific study site can differ greatly from those at the weather station, due to the presence of vegetation, topology, orientation or anthropogenic influences (Bramer et al., 2018). Moreover, a local weather station does not capture fine-scale differences in environmental conditions (i.e., between individual locations within a study site), by collecting data at a standardized, sheltered and shaded location; weather stations deployments explicitly aim to standardise data collection and comparison across large spatial scales. To assess the scale at which individuals sample and respond to their environment, fine-scale high-resolution data collection is necessary. Previous research has studied these small-scale effects in the context of avian breeding biology, but not during the full incubation period, or only during egg-laying (Schaper et al., 2012; Schöll et al., 2020; Shutt et al., 2022). During the full-incubation period, the energetic demands for embryonic development increase, while the necessity for self-maintenance remains. As the associated trade-off and resulting individual decisions are changing throughout, it is important to measure the full period to capture all variation.

Furthermore, ambient temperature provides information on the thermal trade-offs and fitness effects. Additionally, coupled with humidity to calculate heat index (or real-feel temperature), it provides biologically relevant information regarding the costs of thermoregulation and evaporative cooling (Gerson et al., 2014; McKechnie & Wolf, 2019). However, not only external microclimate is an important cue for energetic investment. As natural cavity breeders, the internal conditions are actively modified to suit the eggs' thermal needs (Maziarz, 2019). Due to a discrepancy between the insulation of their natural nesting cavities and the nest boxes, the internal temperature is less buffered from the fluctuations in external temperature (Maziarz et al., 2017). This discrepancy might affect decisions on the incubation behaviour of Pied Flycatchers.

To assess the relevant timescale for decisions on the incubation behaviour of Pied Flycatchers, we asked the following research questions: What is the effect of microclimate on the incubation behaviour across different timescales? Which scale is most relevant for behavioural responses to microclimatic conditions?

As microclimatic conditions are not likely to explain all variation in behavioural responses, we asked these additional questions: What is the effect of relevant breeding parameters (clutch size and lay date) on the incubation behaviour? What is the effect of temporal parameters (calendar date, day of incubation and hour of the day) on the incubation behaviour?

In this study, we predicted that with heat index (real feel) the behavioural response would be different across timescales. Attentiveness is increased regardless of the heat index, as incubation progresses and the embryos develop. Furthermore, we predicted that attentiveness during the active day would decrease with heat index, but would also be less affected with incubation days. See **Table 1** for a more in-depth description of the hypotheses, predictions, predictor variables and the underlying mechanism.

Table 1 Hypothesis table with underlying mechanisms, associated predictions and predictor variables.

Hypothesis	**Mechanism**	**Prediction**	**Predictor variable**
Attentiveness is affected by incubation progression	The embryonic sensitivity to temperature fluctuations increases with progressing development. The female has a breeding itinerary.	Attentiveness will increase with incubation progression	Incubation day
Heat index will affect attentiveness at hour and daily scales	With higher heat index the female can spend more time on the nest as self-maintenance can be reduced. Increased heat index will increase attentiveness till it reaches the thermal neutral zone	Heat index will have a positive effect on attentiveness at hour and daily scales	Heat index external
The interaction between external heat index and UV index will affect incubation behaviour	Increased light intensity results in heating through radiation, coupled with heating through convection as heat index.	Higher UV index with higher heat index will increase nest attentiveness	Heat index external * UV index
The interaction between internal and external heat index will affect incubation behaviour	Colder temperatures outside cool the warmed eggs quicker and colder temperature inside tell the female she has not sufficiently warmed her eggs.	With larger differences between internal and external temperatures, on-bout probability and attentiveness will increase	Heat index internal * heat index external
Clutch size will affect attentiveness	Energetic demands increase with increased clutch size	Larger clutches will result in higher attentiveness	Clutch size
Lay date affects attentiveness across the hour and daily scale	Females experience higher ambient temperatures with later lay dates and have to spend less time on self-maintenance	Later lay dates will result in increased attentiveness at the hour and daily scale.	Lay date
The hour of the active day will have a non-linear relationship with attentiveness for the 4-minute and hour scale.	Self-maintenance is necessary after a full night of incubation and increasing temperatures during the day. Towards the evening ambient temperature decreases and self-maintenance demands have been fulfilled, resulting in higher attentiveness.	The first hours of the day, nest attentiveness will decrease to the minimal required attentiveness to sustain viable egg temperature, to increase towards the evening.	Hour of the active day

Methods

Study species

The Pied Flycatcher (*Ficedula hypoleuca*) is a migratory species travelling from their sub-Saharan non-breeding sites to their European and Western Palearctic breeding sites (Taylor & Christie, 2020). They are a polygynous, hole-breeding species and breed readily in nest boxes. Their preferred habitat consists of mainly woodland and forests with deciduous trees. These trees are suitable for building nests in cavities. Their diet preferences are mostly insects, flying and non-flying, such as flies, beetles, hymenopterans, lepidopterans and bugs. The breeding season spans from late April to the end of June (in Europe). A clutch is usually between 4- 8 eggs and uniparental incubation lasts 13-15 days (Taylor & Christie, 2020). Across Europe, many populations are studied as part of long-term nestbox-monitoring studies, some for more than 50 years (Diez-Méndez et al., 2021; Goodenough et al., 2008; Simmonds et al., 2017; Visser et al., 2021). Variation in breeding behaviours between and within populations shows the adaptability of this species to a changing (small-scale) environment (Lundblad & Conway, 2021; Stonehouse et al., 2023). This makes them a suitable study species for [exploring] the relationship between microclimate and incubation behaviour.

Study site selection

The Hoge Veluwe National Park (The Netherlands; latitude: 52° 04' 60.00" N, longitude: 5° 47' 59.99" E) has been a study site for hole-nesting birds since 1955. The research infrastructure is well-established and Pied Flycatchers breed in nestboxes not occupied by resident species, such as resident Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*). The area is approximately 171 hectares and contains ~350 nestboxes. The study area consists of mixed woodland, interspersed with heathland and walking paths. The vegetation mainly consists of beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*), Northern red oak (*Quercus rubra*), birch (*Betula pendula*.), larch (*Larix kaempferi*.) and pine (*Pinus sylvestris)*, with some vegetation in the understory (as investigated by Schaper et al., 2013). These vegetation characteristics can induce variation in microclimatic conditions, by creating shade, heat storage, or reduced cooling by slowing wind speed.

Sensor-coupled microcontrollers and iButtons

Data collection of behavioural and environmental variables at the nestbox level minimized the discrepancy between measured and local perception scale of Pied Flycatchers. Each nestbox requires an individual sensor to capture fine-scale microclimatic differences. Arduino devices are suitable for this purpose, as they are user-friendly, simple and highly-customizable. The microcontrollers can be programmed to collect data from several attached sensors at specified intervals or threshold triggers. They are used in various applications, measuring climatic conditions (Ardiansah et al., 2021; Cannon et al., 2022; Hilal et al., 2022). The deployed microcontrollers (Arduino Uno Rev3) are connected to sensors, measuring environmental and behavioural factors: UV light intensity (UV Light Sensor Module 200-370nm), ambient temperature and relative air humidity (ASAIR DHT22 sensor AM2302, or: DHT), sound detection (Analog Sound detection sensor) and motion at nestbox entry (PIR-motion sensor). The latter two were not used in the analysis, as they were not correctly measuring nestbox entry or surrounding sound. The microcontrollers are supplied with an SD-card header to store the data. They were placed in inconspicuous, waterproof, permeable containers and attached to the bottom of the nestbox. The light sensor faced the same direction as the opening of the nestbox, receiving similar light conditions. The microcontrollers' program code was written in Arduino IDE v2.3.2 (*Arduino IDE Software*, z.d.). Additionally, iButton temperature loggers (Maxim Device, type DS1925L-F5, accuracy of +-0.0625 ° C at 16-bit) are used to measure the in-nest temperature. They are placed in the nest cup on the outer rim of the clutch, to infer the least disturbance (Podlas and Richner, 2013; Schöll et al, 2020).

Calibration sensors

To measure the sensor and iButton deviation, we used a yearly calibrated temperature and humidity device (Omniport 30 E + E with Eurotec Pro-Com PT2 probe). The DHT-sensors were calibrated at 4, 15 and 21 ° C, following the potential ambient temperature range. The sensors were left to settle for 30 minutes per temperature, before collecting the measurements. Humidity was not controlled for, but ranged from 40.5 (15 ° C) to 94.9 (4 ° C) for the sensor values and 39.3 (15 ° C) to 84.9 (4 ° C) for the calibrated device. The calibrated device values were used to calculate the calibration curve, which was used for the sensor deviation calculations and correction. The iButtons were placed at 23 ° C for 10 minutes, and their deviation was used to adjust the collected data. This temperature was chosen as it was readily available and aligned with the lower limit of incubation temperature.

Sampling design

The nestboxes are selected opportunistically but as equally divided over the research area as possible (n=22). The dataloggers were placed after the first egg was laid but before clutch completion. The iButtons sampled at 4-minute intervals throughout the incubation period (typically between 12-15 days), with a maximum of 22 days. An off-bout period is generally between 7-12 minutes (Conway, 2000; a review by Alvarez and Barba, 2014), thus the sampling interval was set accordingly, to capture off-bout frequency and duration. The Arduino microcontrollers sampled at 30-second intervals to capture all environmental variation before and after off-bouts. Temperature and humidity sensors were placed internally and externally, to capture possible differences in temperature patterns. The sampling period spanned from the 6th of May till the 9th of June 2024.

Breeding and incubation behaviour

First, data from the laying period was collected: the laying date of the first egg (Shutt et al., 2020) and the clutch size at the start of the incubation period. Then, several incubation behaviours were logged and calculated, these include incubation onset (after clutch completion), hatch date, and off-bout frequency and duration to determine attentiveness.

Data analysis

Timescales

For the initial analysis, we used three different timescales. The finest possible scale was 4 minutes, as the iButtons collected incubation data at this interval. The environmental data was assumed to change little within four minutes, therefore the data at the specific matching timestamp was used. For larger timescales, hour and daily scales were chosen, according to Diez-Mendez et al. (2021). To match the environmental variables with the timescales, hour and daily means were calculated.

Incubation behaviour

Incubation behaviour was assessed during the active day, from dawn till dusk, calculated using the *suncalc*-package with the Central European time zone (UTC+2) (Thieurmel & Elmarhraoui, 2022). For the 4-minute scale, the incubation variable was on-bout probability, ranging from 0 (off-bout) to 1 (on-bout). On- and off-bout periods are identified using i*ncR,* an R package specifically designed to assess incubation behaviour based on temperature data (Capilla-Lasheras, 2018) and iButton temperature data. Outliers >45 ˚C were removed, as this exceeds the viable egg temperature. If the recorded internal nest temperature drops at least 1.5 ˚C, it will be considered an off-bout (Walters et al., 2016). Both the number and duration of on- and off-bouts are used to calculate nest attentiveness. For hour and daily scale, the mean duration and sum of the number of off-bouts was calculated for further analysis.

Environmental data

The environmental data from the microcontrollers is used to calculate microclimatic profiles at the nest-box level. Temperature and humidity are used to calculate heat index, also known as real-feel temperature, using the *weathermetrics*- package (Anderson et al., 2016). The UV light index ranges from 0-12, so outliers >12 were removed. Regional environmental data is retrieved from the KNMI weather station Deelen, Hoenderloo (station 275; *Uurwaarden van weerstations*, z.d.).

Statistical analysis

The statistical analyses were performed in R (v 4.3.1; R Core Team, 2023). The external sensor temperature and associated Deelen temperature values were tested for their correlation, using Pearson's correlation test (*stats*-package), to test if the fine-scale temperature differences were captured at the hour-scale, the highest resolution publicly available ($r = 0.70$, $p < 0.001$). Even though they were strongly correlated, indicating a similar pattern in ambient temperature, we used the external sensor temperature data for further analysis, as it was collected at a much higher resolution.

The temporal, behavioural and environmental variables were included in a Generalized Additive (Mixed) Model (GAMM) (see Pedersen et al., 2019 & Wood, 2017 for ecological application and additional background information), using the R-package *mgcv* (Wood, 2023). GAMMs are suitable for our data analysis, as they fit the expected non-linear relationships and can combine fixed and random effects in one model.

For each timescale we built separate models. Then we split each response variable of incubation behaviour: on-bout probability (4-minute scale), attentiveness (hourly and daily scale), number (hourly and daily scale) and duration of off-bouts (hour and daily scale) in separate models. This resulted in seven GAMMs. As predictor variables, we considered the effects of external heat index (˚C) and UV index. We also tested the interaction between external heat index (˚C) and UV index, since we expect sunlight intensity to affect the experienced temperature outside the nestbox (Table 1). Additionally, we tested the interaction between internal and external heat index (˚C), since we expected large differences to have a positive effect on incubation behaviour. Furthermore, we added the breeding parameters: clutch size, lay date and incubation onset. We also included the temporal parameters: hour of the active day and date. Lastly, we added nestbox-ID as a random factor. The model specifications can be found in Appendix 1.

We visualized the model results using the specific plot functions for GA(M)M from *mgcv*. GA(M)M results provide a value for effective degrees of freedom (edf), the closer to 1.00, the more linear the relationship is. They also provide a family-specific statistic and p-value for the fitted relationship. These results combined with the visualization of the models indicate the direction, (non-)linearity, and confidence of the relationships between the predictor and response variables.

Results

In this section, an overview of the descriptive statistics is outlined in **Table 2**. Thereafter, each timescale and corresponding incubation behaviour(s) are sectioned. Additionally, relevant breeding and temporal parameters are mentioned. These conjointly aim to assess the effect of 1) microclimate on the incubation behaviour across different timescales, 2) relevant breeding parameters (clutch size and lay date) on the incubation behaviour and 3) temporal parameters (calendar date, day of incubation and hour of the day) on the incubation behaviour.
At all scales, the response variable for incubation behaviour is different among individual nest boxes (p-values <0.001), except for the duration of off-bouts on the day scale (p= 0.12). The breeding parameters in the model, clutch size and lay date, are not significant at any scale and will not be mentioned in the results hereafter. All model results and additional graphs can be found in Appendix 1 and 2.

***Table 2**. Descriptive statistics for the raw data collected at Hoge Veluwe National Park at nestbox-level, n = 22. The 4-minute scale measured on-bout probability (range 0 -1); therefore, it is not included in this table.*

	Mean ± SD	*Range*
Date	18/05/2024 (±6.6 days)	06/05/2024 – 2024/06/09
Hour of the day (hour)	13.16 (± 4.98)	4 – 22
Environmental parameters		
Heat index internal (˚ C)	18.57(± 5.00)	2.66 - 37.32
Heat index external (˚ C)	18.61 (±4.74)	3.38 - 31.83
UV light index	1.3 (±1.8)	0 - 12.0
Deelen temp (˚ C)	18.06 (±4.06)	4.2 - 27.40
Breeding parameters		
Clutch size	6.6 (±0.94)	4.0 - 8.0
Lay date	04/05/2024 (±6 days)	29/04/2024 - 23/05/2024
Incubation onset	10/05/2024 (±6 days)	06/05/2024 - 27/05/2024
Incubation parameters		
Hour-scale		
Number off-bouts	1.96(±1.14)	0 - 5
Number on-bouts	2.48(±0.96)	0 - 5
Duration off-bouts (minutes)	7.89(±3.76	4.0-60.0
Duration on-bouts (minutes)	23.64(±16.27)	4.0 - 60.0
Attentiveness	0.76(±0.15)	0.00- 1.00
Day-scale		
Number off-bouts	36.5 (±14.5)	6.0 - 70.0
Number on-bouts	37.4 (±14.60)	7.0 - 71.0
Duration off-bouts (minutes)	8.97(±3.72)	6.0 - 50.0
Duration on-bouts (minutes)	38.25 (±26.58)	11.49 - 198.29
Attentiveness (proportion of active day)	0.77(±0.09)	0.53 - 0.96

4-minute scale

Important to note, the r-squared is 0.046, or 4.51% of the deviance is explained by the model. The probability the female will be on the nest increased linearly with a higher heat index (Figure 1a; edf = 1.00, p = 0.06) and in interaction with UV index (Figure 1c; edf = 1.00, p = 0.02). The interaction between internal and external heat index is non-linear and significant, with a higher probability of the female on the nest when it was warmer inside and outside. However, the probability she was on the nest decreased when it was colder outside (Figure 1d; edf = 8.47, p = 0.05). For the hour of the active day, during the morning hours, the on-bout probability decreases, to increase again towards the evening (Figure 1e; edf = 7.25, p < 0.001). Lastly, with incubation days progressing, the on-bout probability non-linearly decreases. First, till day five, the female is less likely to be on the nest. Then, till day nine the probability increases, to decrease again towards hatching (Figure 1f; edf = 4.59, p = 0.01).

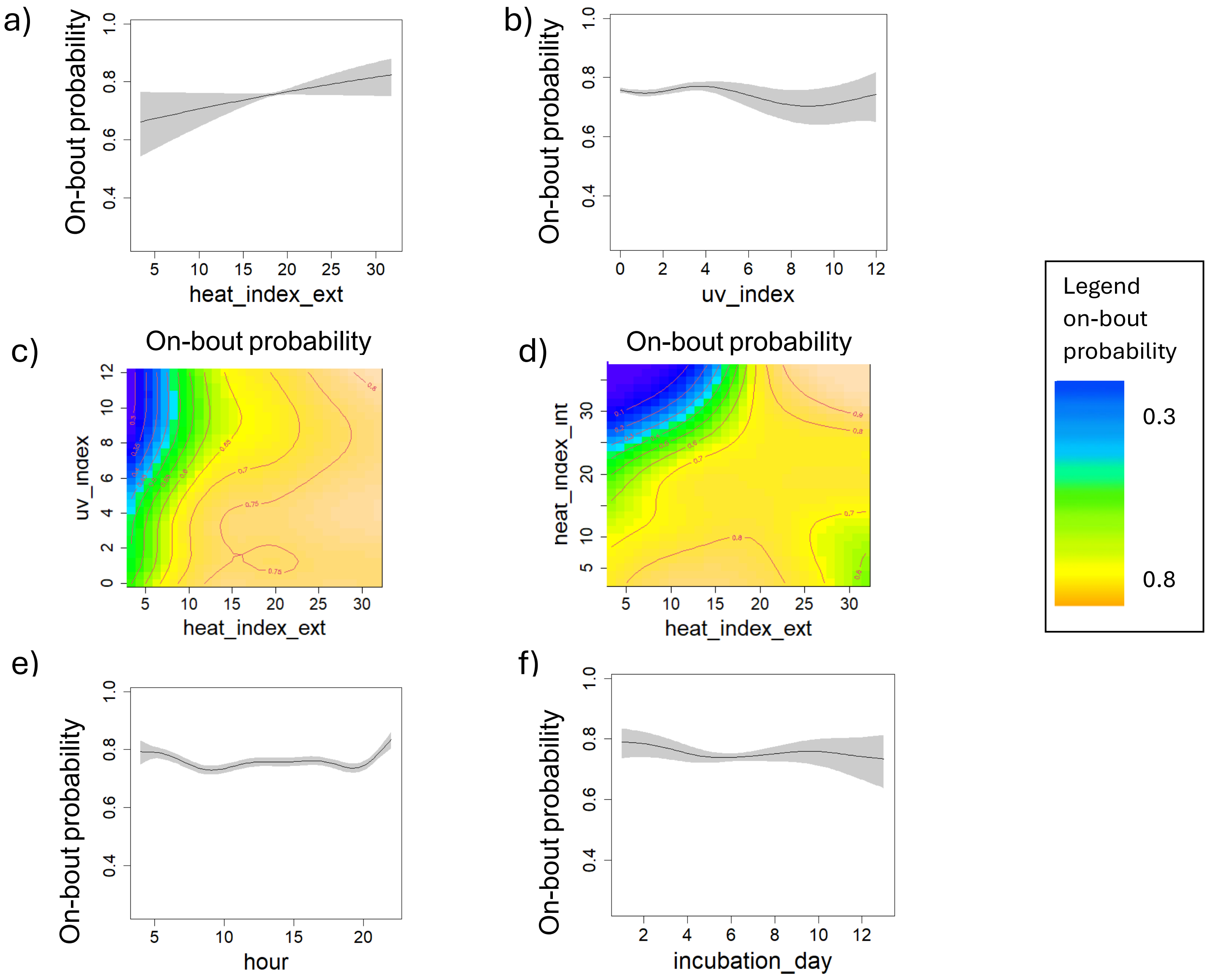


Figure 1. On-bout probability in response to (a) heat index external, (b) UV index, (c) interaction between heat and UV index, (d) interaction between internal and external heat index, (e) hour of the active day and (f) incubation progression.

Hour scale

Attentiveness

Attentiveness increased linearly with hourly heat index, although this was a non-significant effect (Figure 2a; edf = 1.00, p = 0.25). There was no evidence for an hourly UV index effect on nest attentiveness, suggesting that females do not respond to hourly fluctuations in sun exposure (Figure 2b & 2c). However, the interaction between internal and external heat index had a significant effect, with females spending more time on the nest with extreme values inside the nest box and high values outside, and less time on the nest with high values inside and low outside (Figure 2d; edf = 4.54, p = 0.0086). This suggests that females increase their attentiveness based on the heat index outside the nest box, and decrease their attentiveness on the heat index in the nestbox. For the hour of the active day, a similar non-linear pattern to the four-minute scale was found, with spending more time off the nest in the morning and less time in the afternoon (Figure 3a; edf = 7.49, p < 0.001). Lastly, with incubation progression, attentiveness decreased, such that females spent less time on the nest as their eggs approached hatching (Figure 3b; edf = 1.56, p = 0.19).

Number of off-bouts

For heat index, a linear decrease in the number of off-bouts is found (Figure 2a; edf = 1.00, p = 0.0027), but for UV index or the interaction this effect is not found, suggesting the females respond to hourly heat index but not sun exposure. Furthermore, the interaction between internal and external heat index had a significant effect, with females leaving the nest less often with extreme values inside the nest box and high values outside, and leaving more often with low values inside and high outside (Figure 2d; edf = 3.81, p < 0.001). This suggests that females decrease their hourly number of off-bouts based on the heat index outside the nestbox, and increase it based on the heat index inside the nestbox. The hour of the active day showed a pattern inverse to the attentiveness, with the female leaving the nest more often in the morning and less towards the evening (Figure 3a; edf = 8.189, p <0.001). Lastly, the number of off-bouts increased as the eggs approached hatching, thus the female left the nest more often (Figure 3a; edf = 1.88, p = 0.12).

Duration of off-bouts

No significant effect was found for both heat index and UV index, as well as their interaction terms, suggesting females do not respond to hourly environmental variation by adjusting the duration of their off-bouts (Figure 2a-d; p-value 0.32- 0.53). The hour of the active day showed a non-linear pattern, with shortening off-bouts in the morning and extending off-bouts towards the evening (Figure 3a; edf = 5.62, p <0.001). Lastly, incubation progression showed a non-linear pattern, with females shortening their off-bouts till halfway through their incubation period and extending as the hatching date approached (Figure 3a; edf = 3.23, p = 0.018).

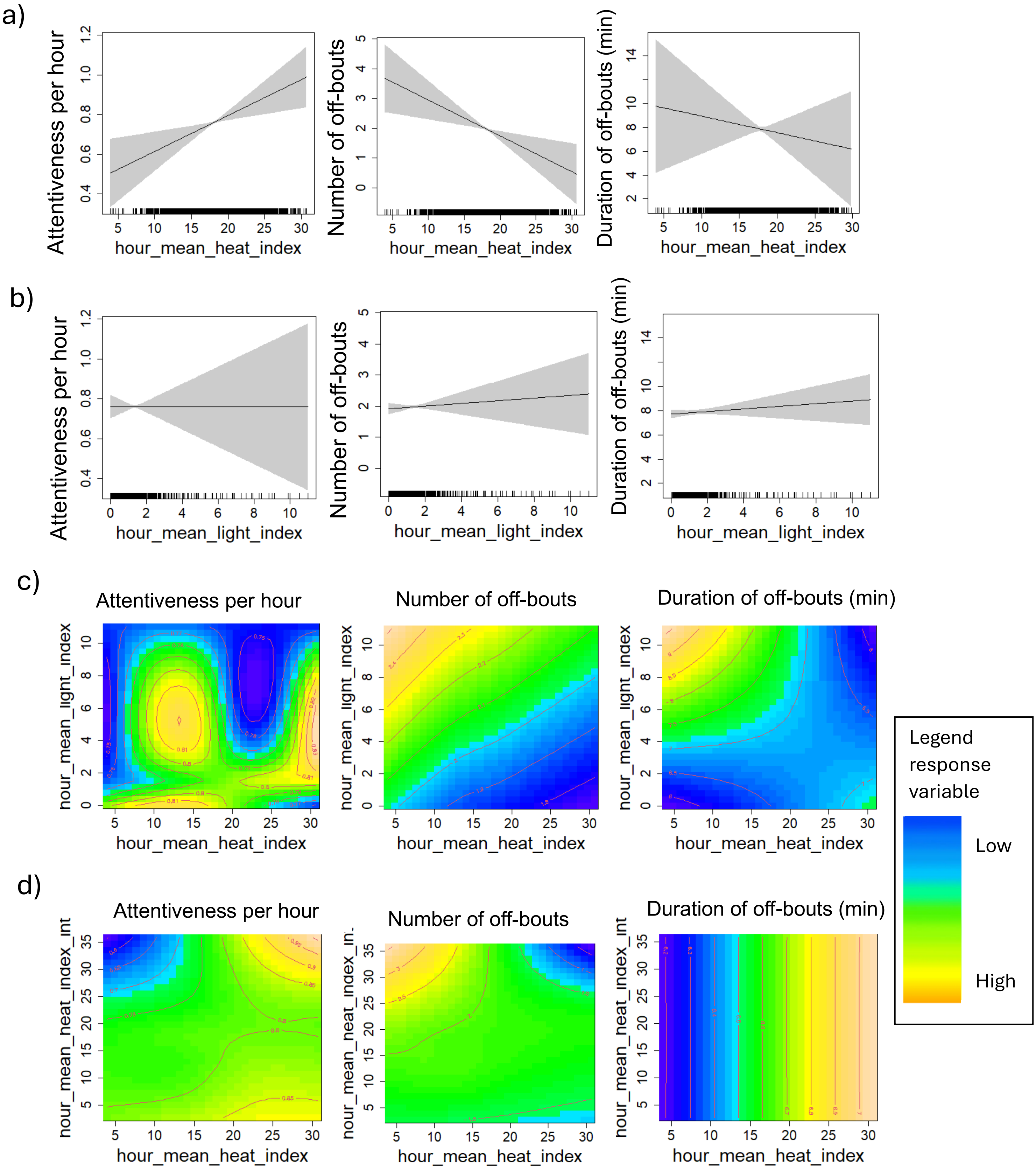


Figure 2. Environmental variables and behavioural responses
The hourly nest attentiveness (l), number of off-bouts (m) and duration of off-bouts (r), in response to (a) heat index, (b) UV index, (c) interaction between heat and UV index, (d) interaction between internal and external heat index, Hourly heat index is by default external heat index. The colours in the interaction graphs range from blue (low values) to orange (high values) for the response variable.

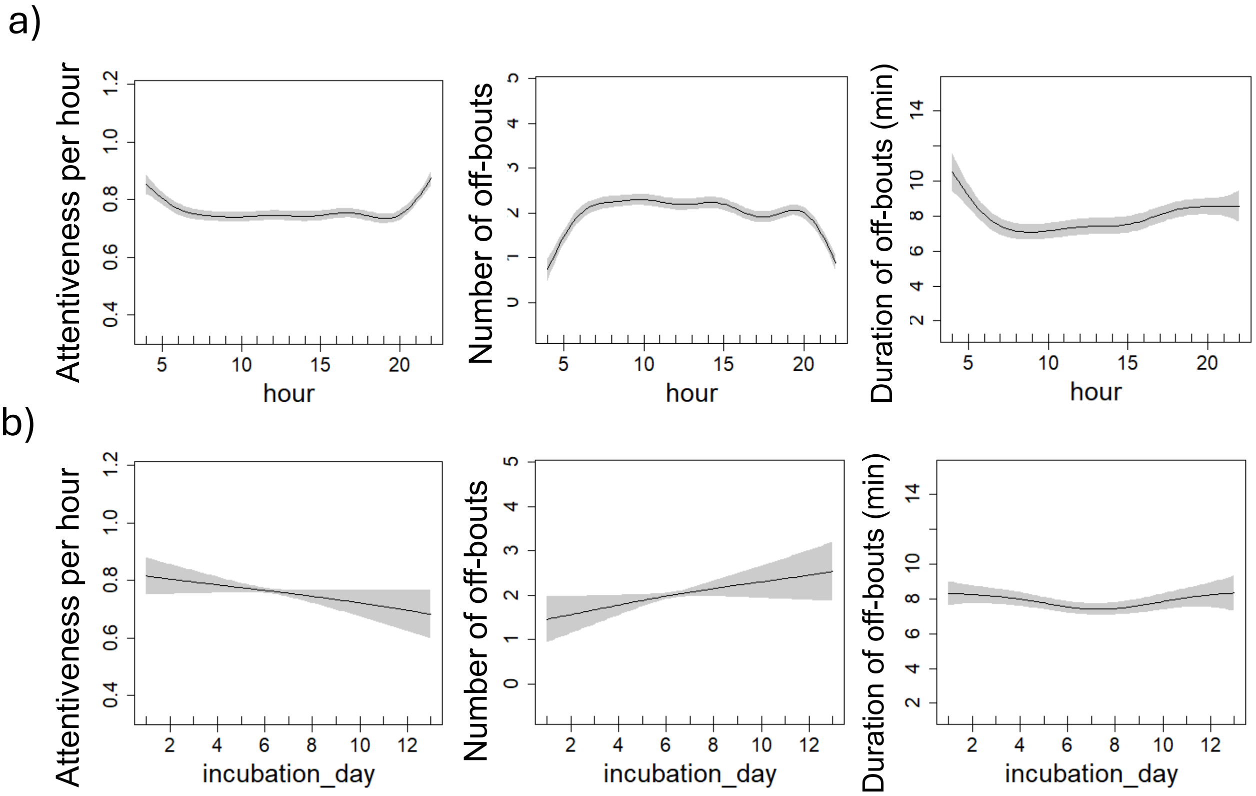


Figure 3. Temporal parameters and behavioural responses
The hourly nest attentiveness (l), number of off-bouts (m) and duration of off-bouts (r), in response to (a) hour of the active day and (b) incubation progression, mentioned as incubation day.

Daily scale

Attentiveness

All predictor variables and interactions are not significant for attentiveness. Nonetheless, the interaction between UV index and heat index outside the nestbox suggests that the female only increased her daily attentiveness when it was perceivably warmer with a high sunlight intensity (Figure 4c). Furthermore, the attentiveness decreased when the heat index inside was high, but outside was low. However, when it was high both inside and outside, or just low inside, she increased her attentiveness (Figure 4d). This suggests she reacted differently to perceived temperatures inside the nestbox, but not to those outside the nestbox (Figure 4d). Lastly, as the incubation period progresses, the female first increases attentiveness, to decrease it again from mid-incubation till hatching (Figure 4e).

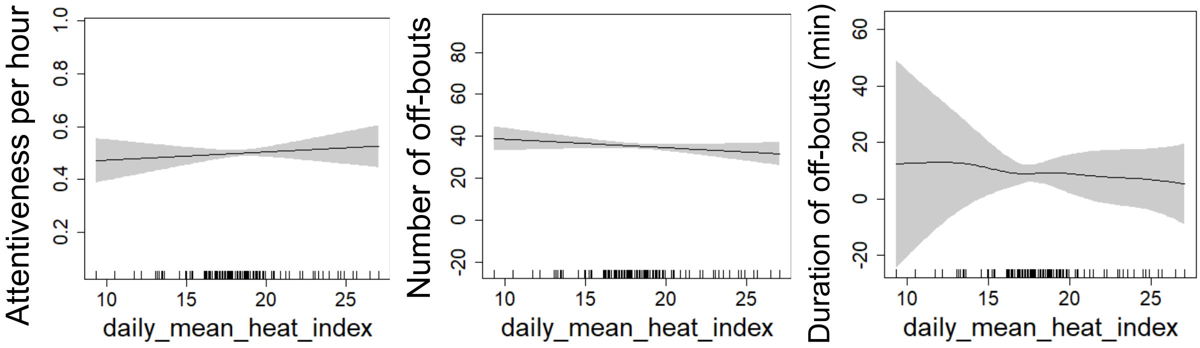
Number off-bouts

The females decreased the number of off-bouts per day with a higher heat index outside, regardless of the heat index inside the nestbox (Figure 4a & 4d). Conversely, when the UV index increased, the female left the nest more often, except when the heat index was also higher (Figure 4b & 4c). However, these environmental variables all had a non-significant effect (p-values 0.19 - 0.88). Furthermore, as eggs approached hatching, the female left the nest less often, because the number of off-bouts decreased significantly (Figure 4e; edf = 2.20, p = 0.0098).

Duration off-bouts

The main effects of heat index and UV index are not significant, but their interactions are. First, regardless of UV index the duration of off-bouts was short, except for high heat index with low UV index. In other words, the female took longer off-bouts when it was perceivably warmer with lower sunlight intensity (Figure 4c; edf = 11.40, p <0.001). Second, for the interaction between the heat index inside and outside the nestbox, we found a non-linear effect. It shows the female extends her off-bouts when the heat index inside the nestbox is considerably higher than outside. However, when the heat index is high outside, and either low or high inside, she shortens her off-bouts (Figure 4d; edf = 1.75, p = 0.07). Lastly, the female shortened her off-bouts when approaching the hatching date (Figure 4e; edf = 2.99, p = 0.009).

a)



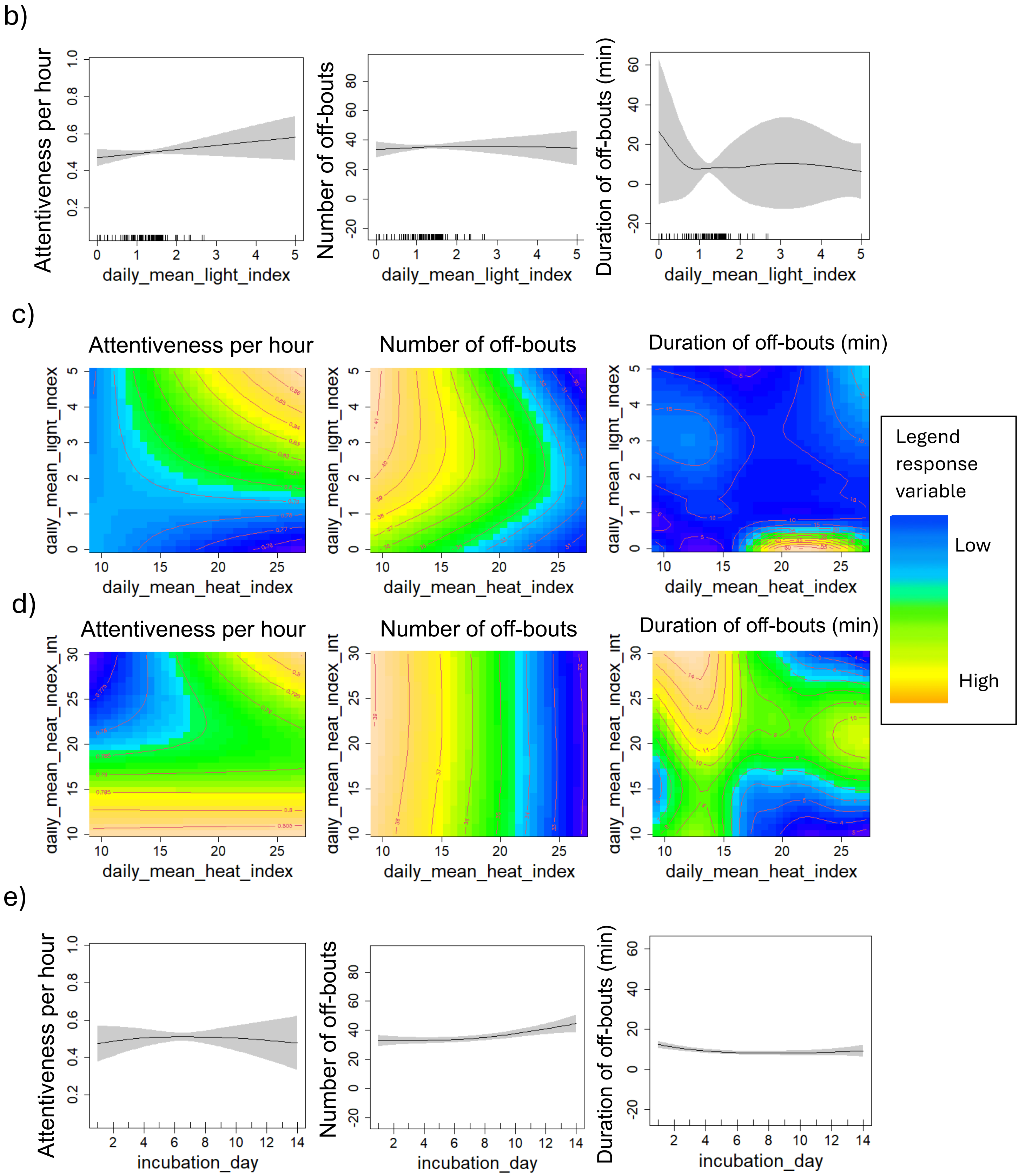


Figure 4. Environmental and temporal variables to behavioural responses

The daily nest attentiveness (l), number of off-bouts (m) and duration of off-bouts (r), in response to (a) heat index, (b) UV index, (c) interaction between heat and UV index, (d) interaction between internal and external heat index and (e) incubation progression, mentioned as incubation day. Daily heat index is by default external heat index. The colours in the interaction graphs range from blue (low values) to orange (high values) for the response variable.

Discussion

In this study, we wanted to assess the relevant timescale for decisions on the incubation behaviour of Pied Flycatchers. This in relation to the microclimatic conditions, breeding parameters and temporal parameters.

The incubation behaviour in response to the microclimatic conditions differed across the timescales. Similarly for the temporal parameters on the incubation behaviour. Not all variables are significant on all timescales, they might not be relevant in determining the behaviour on that particular timescale (e.g. a specific itinerary is more influential than the weather on day/incubation daily scale). Important to note before interpreting the results: the low R-squared (R.sq = 0.046) at the 4-minute scale suggests that the variation can only be partially explained by the parameters included in the model. Similarly, the duration of off-bouts per hour was low (R.sq. = 0.06). At the hour- and daily scale the (other) incubation behavioural responses were much higher (0.39-0.84), thus these can be predicted by the environmental and individual (breeding) variation we included in the model.

In line with our expectations, we found that attentiveness increased with heat index across all scales. At the daily and hourly scale, higher attentiveness is achieved by decreasing the number and duration of off-bouts. The warmer at any moment during the day, the less and shorter the female has to leave to forage and self-maintain. This is in line with previous research investigating microclimatic conditions at nestbox- and site-level in Tree Swallows (*Tachicineta bicolor*) and Great Tits, respectively (Coe et al., 2015; Schöll et al., 2020). However, other studies found the opposite effect, but temperature data was collected at weather station-level and is less likely to capture the variation individuals experience (Amininasab et al., 2016; Diez-Méndez et al., 2021). On the 4-minute scale, the on-bout probability increases, likely due to the same energy constraints she experiences at large timescales. The trade-off between self-maintenance and reproductive investment is likely similar across these scales. This suggests a smaller timescale shows the fine-scale variation in heat index, but the effect on a behavioural decision is fairly small (r-sq. = 0.045). At a large scale, daily or incubation period, the female likely follows a certain breeding 'itinerary', with fewer deviations in response to the perceived temperature, and only by adjusting the off-bout duration (Conway, 2000; Diez-Méndez et al., 2021). The hour scale shows more flexibility and adaptability to adjust incubation behaviour to the hourly variation in heat index, but a strategy is observed. The relevant scale for heat index would be between four minutes and an hour, to capture all fine-scale microclimatic variation with a higher explained variation in incubation behavioural decisions.

As environmental variables interact in the microclimate, we found this interaction to have a non-linear, positive effect on incubation behaviour. The females showed a similar nest attentiveness to the heat index when it was warmer and sunnier during the day. However, when we look at the hourly pattern, the female increases her attentiveness in different scenarios. Both moderate and warm hours with moderate sunlight intensity lead the female to spend more time on the nest. Only with a very high UV index, she increased the number and duration of off-bouts, but less when the heat index was also high. These results show the variability and adaptability on the hour scale, which is less observed daily. Unfortunately, this interaction has not been studied previously. Based on our findings, we would suggest the hourly scale would be the relevant scale for this interaction.

Partly in line with our expectations, a large difference in temperature between internal and external, with a positive effect on the on-bout probability and attentiveness was only found for low internal and high external heat index for all timescales. The increased attentiveness was also found with both high internal and external heat index. In other words, the female was more on the nest, when it was warmer outside. This could be due to a decreased need for foraging, resulting in incubation investment. The opposite was also true, when it was warmer inside, the female spent less time on the nest. Previous research found that by warming nests by a few degrees (1- 2.5), energy constraints were slightly alleviated, leading to reduced attentiveness, similar to our findings (Arct et al., 2022; Mueller et al., 2019). Since timescales hardly differed, we would suggest none to be more relevant.

Contrary to our expectations, no effect of clutch size on incubation behaviour was found at any scale. Attentiveness did not increase, in line with previous research in Blue Tits and Great Tits (Amininasab et al., 2016; Bambini et al., 2019; Diez-Méndez et al., 2021; Diez-Méndez et al., 2021; Schöll et al., 2020). Nonetheless, it is expected that the larger the clutch size, the more energy is needed to heat the eggs. As a result, the larger clutch size retains its temperature for longer (Boulton & Cassey, 2012; Reid et al., 2000). However, with additional eggs, the metabolic rate increased, even more so with lower (ambient) temperatures (Haftorn & Reinertsen, 1985). There is likely a balance between reduced cooling rates and costs of additional eggs, explaining why this effect is not often observed.

Lay date does not affect incubation behaviour, even though later females were expected to experience pressure from their environment to shorten their incubation, e.g. through lower food abundance, higher overall temperatures and lesser territory availability (Shutt et al., 2022). However, this effect might be less for Pied Flycatchers, as they are a migratory species and have a shorter window of opportunity nonetheless. Furthermore, their diet is also much more diverse compared to Great Tits, so their timing is less dependent on the peak in caterpillar abundance. Therefore, a mismatch with peak food abundance of a certain order of insects might have less adverse effects on their breeding success.

As expected, the hour of the active day had a non-linear relationship with attentiveness for the 4-minute and hour scale. We found that the female is less on the nest in the morning and more towards the evening How this attentiveness pattern is achieved, differs among studies; through initial off-bout duration increase and later decrease, similar to our results, in Great Tits (Conway, 2000; Diez-Méndez et al., 2021), or through an increase in duration and decrease in the number of off-bouts, observed in Carolina Chickadees (Walters et al., 2016). This could be explained by the need for foraging after a night of continuous incubation and higher ambient temperatures during the day. Additionally, prey emergence and availability might be higher in the morning, resulting in higher hunting success rates. Unfortunately, there are few studies on hourly and daily insect emergence and availability patterns. As these patterns are observed across the hour and 4-minute scale, the relevant scale is likely in between.

As incubation progresses, the energetic investment for embryonic development increases. This can be achieved through shortening off-bouts and decreasing the number of off-bouts, resulting in an overall higher nest attentiveness (Bambini et al., 2019; Diez-Méndez et al., 2021; Simmonds et al., 2017). Contrary to our expectations, we found that nest attentiveness slightly decreased with incubation progression, across all timescales. Other studies found no effect of attentiveness (Álvarez & Barba, 2014; Conway, 2000), but not decreased attentiveness. This could be due to experienced predation risk or decreased food availability and quality, necessitating more and longer off-bouts. However, the off-bout duration and number of off-bouts per hour and day decreased, showing a breeding strategy for more and shorter off-bouts towards hatching. The 4-minute and hourly scale showed the females spent less time on the nest. Few studies investigated the hourly or even minute-scale and found the opposite of our results in Great Tits (Diez-Méndez et al., 2021). This could be due to differences in species, as Pied Flycatchers breed slightly later and might have lower food availability or quality. Furthermore, we found that females increased the daily number of off-bouts but shortened them when the hatching date approached. Likely the hour-scale does not capture the strategy adopted for the incubation progression when comparing it to the daily scale. There can be variation on the hour scale resulting in a similar daily pattern. Based on these results, the relevant timescale for incubation progression is likely between hourly and daily scale.

These findings suggest that different timescales are important for different incubation behaviours. Furthermore, the breeding and temporal parameters are relevant in explaining behavioural patterns observed across timescales. To capture most variation explained by environmental variables and temporal parameters, the current scale range (4 minutes to daily) is a good starting point for disentangling these relationships.

However, to conclude which timescale best predicts the incubation behaviour, a sliding window approach with different timescales, similar to Simmonds et al. (2017), could provide a complete and thorough answer. This might be different for each component of the incubation behaviour. Furthermore, we assume birds base their behavioural decisions on the temporal environmental variation at the nestbox level and not the weather-station level, as discussed in the introduction. However, including different spatial scales, such as territory- (Shutt et al., 2022) or study site-level, could explain more about the behavioural response to environmental variation. This could be investigated using a similar sliding window approach.

Additionally, it would be interesting to combine these outcomes and be able to predict the probability a female will leave the nest, at certain environmental conditions. An environmental factor that might prove to be important, but was not considered in this study is precipitation. Some studies found negative effects of precipitation (Burant et al., 2024; Coe et al., 2015), while others failed to find a significant effect (Schöll et al., 2020). Also, pied flycatchers are uniparental incubators but have a partner carrying some of the energetic costs by feeding the female during incubation. This male feeding increases with lower ambient temperature but decreases with very low temperatures (2-5 degrees Celsius). However, it is constricted by nest predation, so the relative contribution to behavioural responses is still questioned (Amininasab et al., 2016; Bambini et al., 2019; Martin & Ghalambor, 1999). For further investigation of the relationship between microclimate and incubation behaviour at different temporal (and spatial) scales, we would recommend studying multiple populations at several sites, as results can differ with latitude (Álvarez & Barba, 2014; Lundblad & Conway, 2021), vegetation (Diez-Méndez et al., 2021; Kim et al., 2022) and species (Conway, 2000; Mueller et al., 2019; Shutt et al., 2022; Williams et al., 2023).

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Appendix

1. Model results

1.1 4-minute scale

```
Family: binomial 
Link function: logit 

Formula:
incR_score ~ s(heat_index_ext, k = 15) + s(uv_index, k = 10) + 
    te(heat_index_ext, uv_index) + te(heat_index_ext, heat_index_int) + 
    s(incubation_day) + s(LayDate, k = 3) + s(hour) + s(year_date) + 
    s(ClutchSize, k = 3) + s(box_no, bs = "re")

Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept)    1.137      0.177   6.422 1.35e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                     edf Ref.df  Chi.sq  p-value    
s(heat_index_ext)                  1.006  1.011   3.382 0.065901 .  
s(uv_index)                        4.185  4.987  13.092 0.024814 *  
te(heat_index_ext,uv_index)        1.026  1.050   5.449 0.022449 *  
te(heat_index_ext,heat_index_int)  8.465 21.000  84.427 0.050784 .  
s(incubation_day)                  4.588  5.668  15.975 0.010177 *  
s(LayDate)                         1.001  1.001   1.158 0.281867    
s(hour)                            7.253  8.258  48.242  < 2e-16 ***
s(year_date)                       4.579  5.659  26.563 0.000168 ***
s(ClutchSize)                      1.000  1.000   1.166 0.280302    
s(box_no)                         10.224 11.000 619.323  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Rank: 111/112
R-sq.(adj) =  0.0462   Deviance explained = 4.51%
-REML =  14911  Scale est. = 1         n = 27379
```

1.2 Hour scale

1.2.1 Attentiveness

```
Family: gaussian 
Link function: identity 

Formula:
attentiveness_hour ~ s(hour_mean_heat_index, k = 15) + s(hour_mean_light_in
dex) + 
    te(hour_mean_heat_index, hour_mean_light_index) + te(hour_mean_heat_ind
ex, 
    hour_mean_heat_index_int) + s(year_date) + s(hour) + s(ClutchSize, 
    k = 3) + s(LayDate, k = 3) + s(incubation_day) + s(box_no, 
    bs = "re")

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.76081    0.02455   30.99   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                edf  Ref.df      F p-v
alue    
s(hour_mean_heat_index)                      1.0002  1.0004  1.302  0.
2539    
```

```
s(hour_mean_light_index)                            1.0004  1.0005  0.349  0.
5551
te(hour_mean_heat_index,hour_mean_light_index)      5.6650  7.6181  1.517  0.
2267
te(hour_mean_heat_index,hour_mean_heat_index_int) 4.5388 21.0000  1.508  0.
0086 **
s(year_date)                                        4.5233  5.5341  2.257  0.
0370 *
s(hour)                                             7.4879  8.4358 14.274  <2
e-16 ***
s(ClutchSize)                                       1.0001  1.0001  0.335  0.
5627
s(LayDate)                                          0.2527  0.2658  1.273  0.
5609
s(incubation_day)                                   1.5609  1.9292  1.810  0.
1971
s(box_no)                                           9.8680 11.0000 31.569  <2
e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Rank: 111/112
R-sq.(adj) =  0.383   Deviance explained = 39.8%
-REML =  -1085  Scale est. = 0.012701  n = 1519
```

1.2.2 Number of off-bouts

```
Family: gaussian
Link function: identity

Formula:
number.off.bouts ~ s(hour_mean_heat_index, k = 10) + s(hour_mean_light_inde
x,
    k = 10) + te(hour_mean_heat_index, hour_mean_light_index) +
    te(hour_mean_heat_index, hour_mean_heat_index_int) + s(year_date) +
    s(hour) + s(ClutchSize, k = 3) + s(LayDate, k = 3) + s(incubation_day)
+
    s(box_no, bs = "re")

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   1.9758     0.1961   10.07   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                        edf    Ref.df      F
p-value
s(hour_mean_heat_index)                              1.000198 1.000e+00  8.97
6 0.002776 **
s(hour_mean_light_index)                             1.001178 1.002e+00  0.39
4 0.529911
te(hour_mean_heat_index,hour_mean_light_index)       1.003395 1.007e+00  0.01
1 0.935296
te(hour_mean_heat_index,hour_mean_heat_index_int)  3.818065 2.100e+01  2.63
2 0.000343 ***
s(year_date)                                         4.720578 5.762e+00  2.98
5 0.006159 **
s(hour)                                              8.188569 8.822e+00 32.49
5  < 2e-16 ***
s(ClutchSize)                                        1.016563 1.018e+00  1.17
4 0.275421
s(LayDate)                                           0.000557 5.902e-04  0.73
9 0.983343
s(incubation_day)                                    1.883790 2.382e+00  2.08
0 0.117337
s(box_no)                                           10.235606 1.100e+01 44.23
4  < 2e-16 ***
---
```

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Rank: 106/107
R-sq.(adj) =  0.472   Deviance explained = 48.4%
-REML = 1897.6  Scale est. = 0.66005   n = 1519
```

1.2.3 Duration of off-bouts

```
Family: gaussian 
Link function: identity 

Formula:
mean.time.off.bout ~ s(hour_mean_heat_index) + s(hour_mean_light_index, 
    k = 10) + te(hour_mean_heat_index, hour_mean_light_index) + 
    te(hour_mean_heat_index, hour_mean_heat_index_int) + s(year_date, 
    k = 3) + s(hour) + s(ClutchSize, k = 3) + s(LayDate, k = 3) + 
    s(incubation_day) + s(box_no, bs = "re")

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)   7.8539     0.1732   45.35   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                       edf  Ref.df     F  p
-value    
s(hour_mean_heat_index)                           1.000755  1.0015 0.472 0.
492030    
s(hour_mean_light_index)                          1.000336  1.0007 0.987 0.
320517    
te(hour_mean_heat_index,hour_mean_light_index)    1.003063  1.0060 0.732 0.
393600    
te(hour_mean_heat_index,hour_mean_heat_index_int) 0.002158 21.0000 0.000 0.
531819    
s(year_date)                                      1.000120  1.0002 0.029 0.
863953    
s(hour)                                           5.620279  6.7834 7.327  <
2e-16 ***
s(ClutchSize)                                     1.000091  1.0001 1.482 0.
223685    
s(LayDate)                                        0.142587  0.1829 0.910 0.
683385    
s(incubation_day)                                 3.233643  4.0297 3.025 0.
017840 *  
s(box_no)                                         5.155214 11.0000 1.496 0.
000793 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Rank: 99/100
R-sq.(adj) =  0.0698   Deviance explained = 8.33%
-REML =   3522  Scale est. = 11.596    n = 1327
```

1.3 Daily scale

1.3.1 Attentiveness

```
Family: Beta regression(99.029) 
Link function: logit 

Formula:
attentiveness_day ~ s(daily_mean_heat_index) + s(daily_mean_light_index) + 
    te(daily_mean_heat_index, daily_mean_light_index) + te(daily_mean_heat_
index, 
    daily_mean_heat_index_int) + s(LayDate, k = 3) + s(incubation_day) + 
    s(year_date) + s(ClutchSize, k = 3) + s(box_no, bs = "re")
```

```
Parametric coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)    1.352      0.151   8.951   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                      edf Ref.df  Chi.sq p-
value
s(daily_mean_heat_index)                            1.000  1.000   0.456 0.
49952
s(daily_mean_light_index)                           1.000  1.000   1.738 0.
18738
te(daily_mean_heat_index,daily_mean_light_index)    1.000  1.000   0.349 0.
55499
te(daily_mean_heat_index,daily_mean_heat_index_int) 0.708 18.000   2.707 0.
14072
s(LayDate)                                          1.044  1.045   1.363 0.
22773
s(incubation_day)                                   2.250  2.850   2.768 0.
45575
s(year_date)                                        3.584  4.570  14.530 0.
00775 **
s(ClutchSize)                                       1.288  1.303   1.109 0.
35409
s(box_no)                                            9.948 11.000 179.976 <
2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Rank: 97/98
R-sq.(adj) =  0.846   Deviance explained = 87.5%
-REML = -158.1  Scale est. = 1         n = 106
```

1.3.2 Number of off-bouts

```
Family: gaussian
Link function: identity

Formula:
number.off.bouts ~ s(daily_mean_heat_index) + s(daily_mean_light_index,
    k = 10) + te(daily_mean_heat_index, daily_mean_light_index) +
    te(daily_mean_heat_index, daily_mean_heat_index_int) + s(LayDate,
    k = 3) + s(incubation_day) + s(year_date, sp = 3, k = 10) +
    s(ClutchSize, k = 3) + s(box_no, bs = "re")

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   35.229      4.021   8.761 1.49e-13 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                        edf Ref.df      F p
-value
s(daily_mean_heat_index)                             1.0016  1.003  1.749 0
.18886
s(daily_mean_light_index)                            1.3935  1.644  0.161 0
.74280
te(daily_mean_heat_index,daily_mean_light_index)     1.2901  1.521  0.057 0
.88254
te(daily_mean_heat_index,daily_mean_heat_index_int)  0.1163 21.000  0.007 0
.30697
s(LayDate)                                           1.0001  1.000  1.364 0
.24596
s(incubation_day)                                    2.2054  2.756  4.085 0
.00981 **
```

```
s(year_date)                                         0.3624  0.629  0.136 0
.77071
s(ClutchSize)                                        1.0001  1.000  2.456 0
.12074
s(box_no)                                           10.4280 11.000 28.444 <
2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Rank: 97/98
R-sq.(adj) =  0.832   Deviance explained = 86.2%
-REML = 354.18  Scale est. = 41.075    n = 106
```

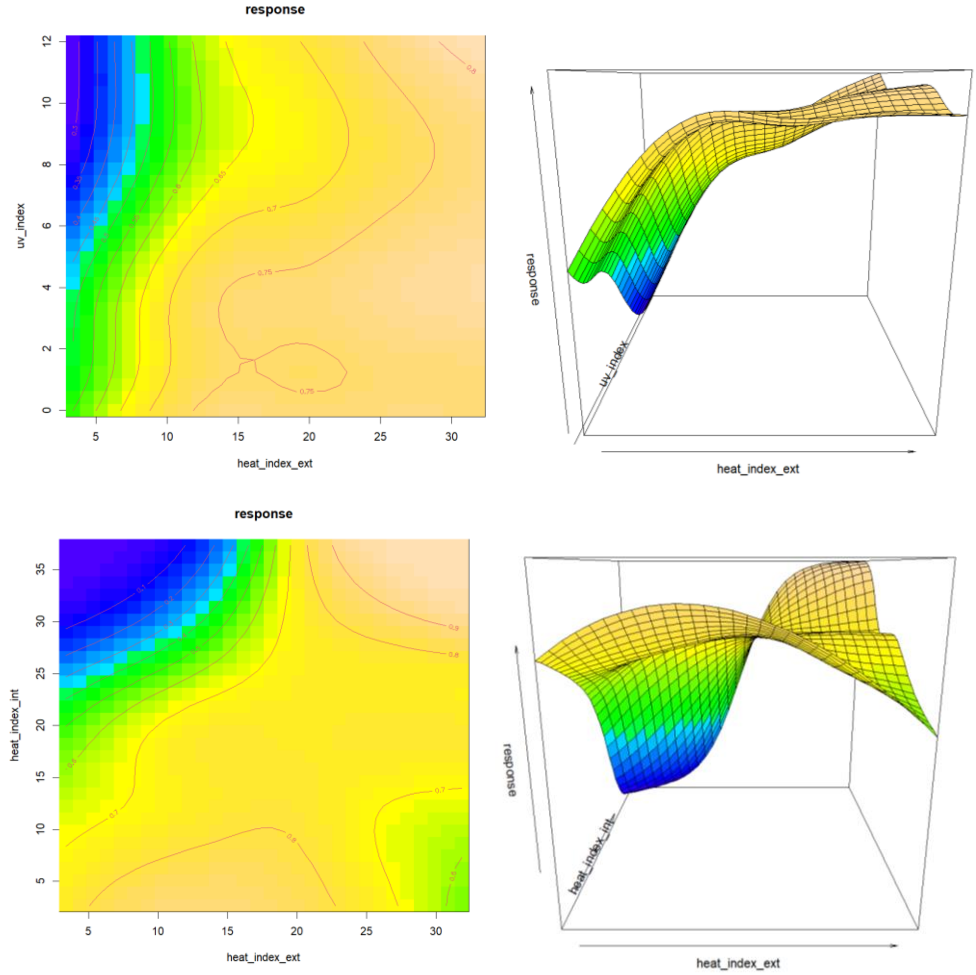
1.3.3 Duration of off-bouts

```
Family: gaussian
Link function: identity

Formula:
mean.time.off.bout ~ s(daily_mean_heat_index) + s(daily_mean_light_index) +
    te(daily_mean_heat_index, daily_mean_light_index) + te(daily_mean_heat_
index,
    daily_mean_heat_index_int) + s(LayDate, k = 3) + s(incubation_day) +
    s(year_date, sp = 2, k = 10) + s(ClutchSize, k = 3) + s(box_no,
    bs = "re")

Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)    9.156      0.312   29.35   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                                                      edf  Ref.df     F  p
-value
s(daily_mean_heat_index)                            2.859  3.6415 0.207  0
.95231
s(daily_mean_light_index)                           5.033  5.9847 1.332  0
.25876
te(daily_mean_heat_index,daily_mean_light_index)   11.399 12.6355 4.646 1.
87e-05 ***
te(daily_mean_heat_index,daily_mean_heat_index_int)  1.749 20.0000 0.194  0
.07542 .
s(LayDate)                                          1.000  1.0002 0.550  0
.46042
s(incubation_day)                                   2.991  3.7083 3.711  0
.00882 **
s(year_date)                                        0.384  0.6347 0.279  0
.67495
s(ClutchSize)                                       1.651  1.8143 2.199  0
.13490
s(box_no)                                           2.159 11.0000 0.284  0
.12065
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Rank: 97/98
R-sq.(adj) =  0.683   Deviance explained = 77.1%
-REML = 276.34  Scale est. = 6.3344    n = 106
```

2. Graphs

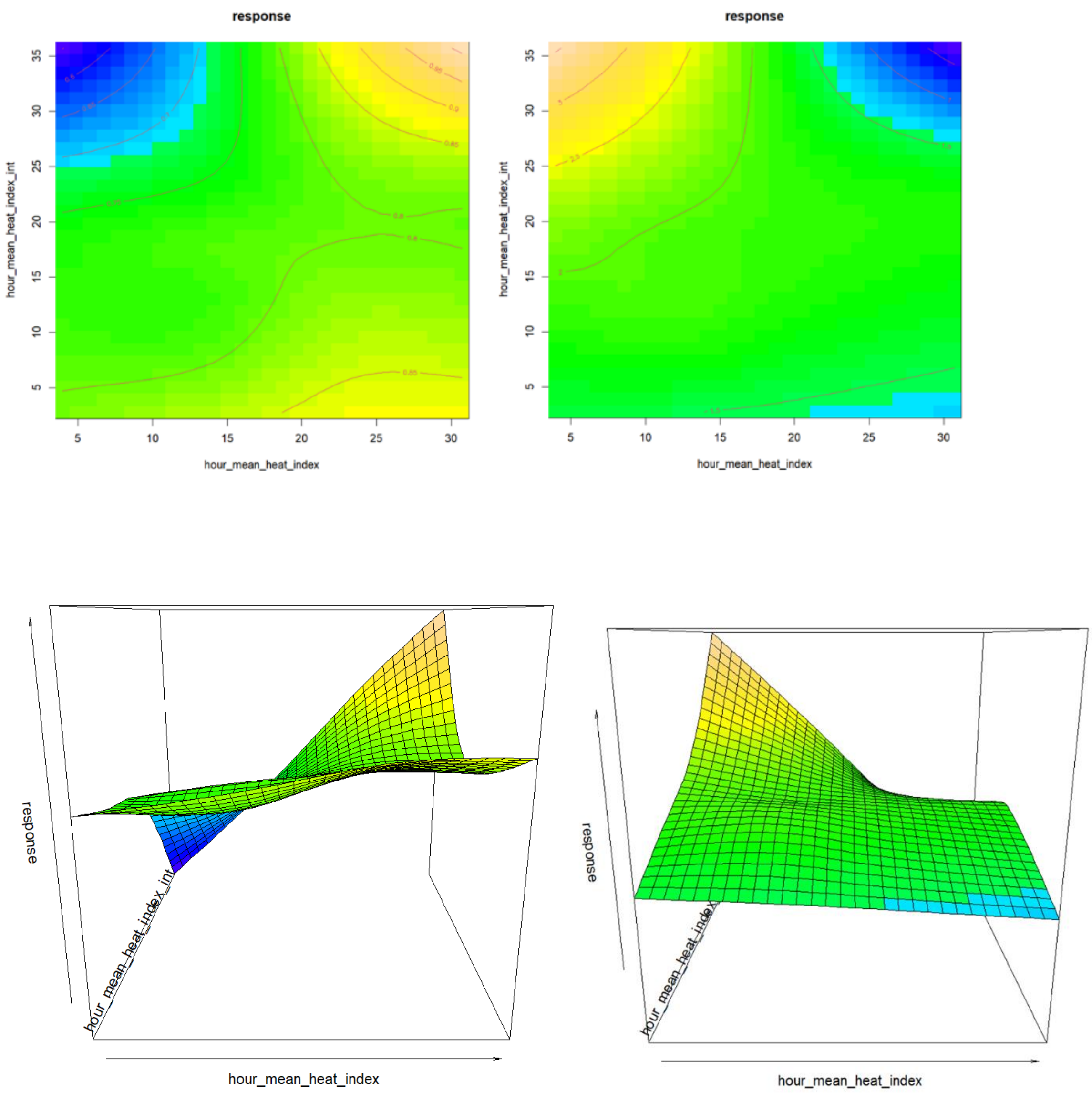
2.1 3D-graphs of interactions

2.1.1 4-minute scale



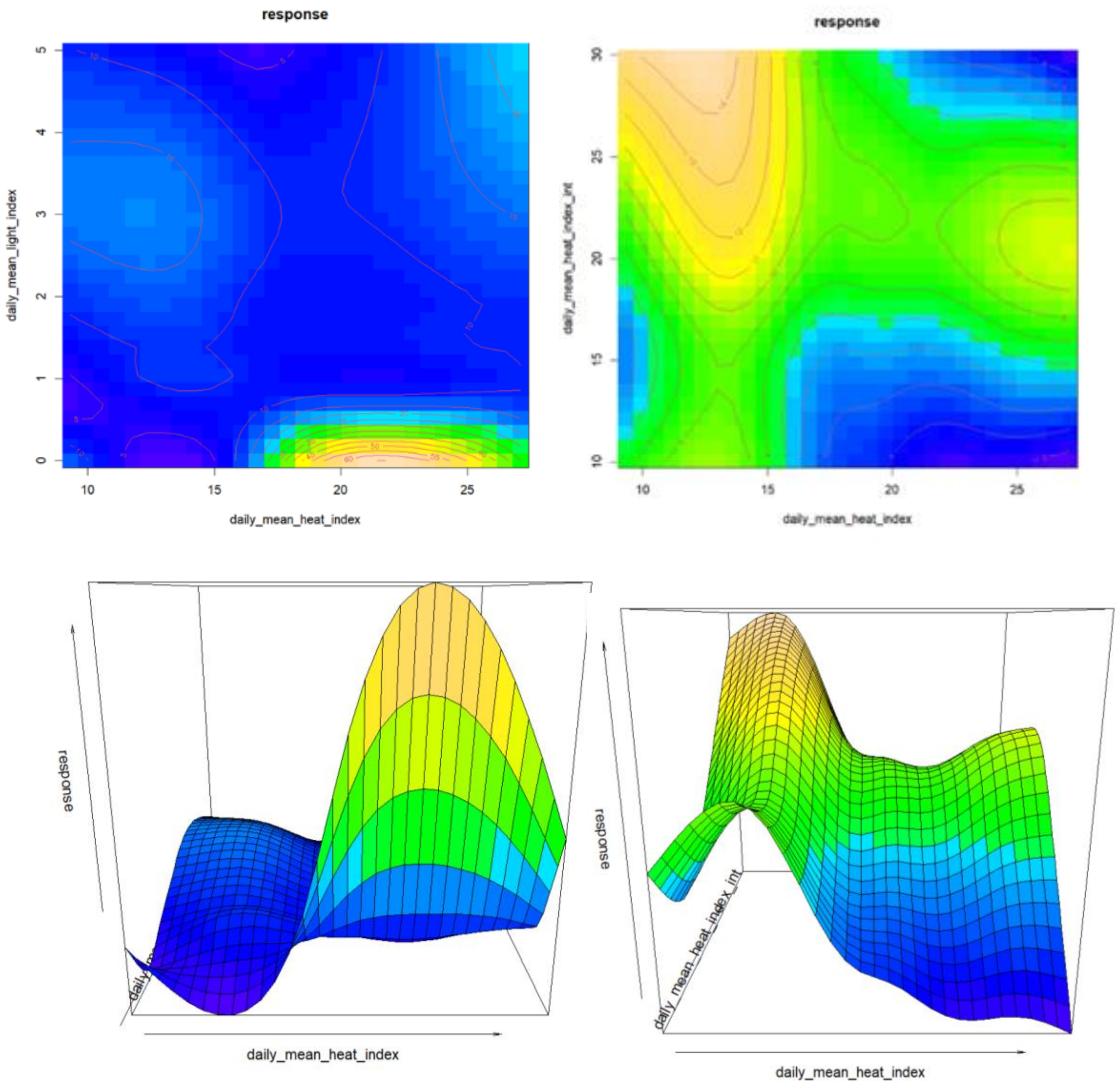
4-minute On-bout probabilty in response to the interaction between UV-index and external heat index, and the interaction between internal and external heat index

2.1.2 Hour scale



HOUR Attentiveness and number of off-bouts in response to the interaction between internal and external heat index

2.1.3 Daily scale

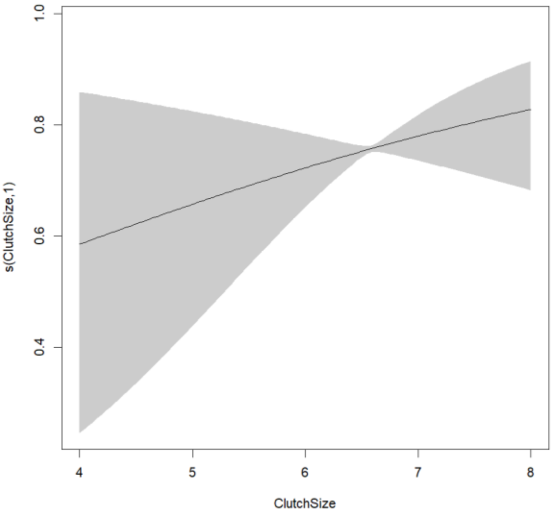


DAILY duration of off-bouts in response to the interaction between external heat index and UV-index, and the interaction between internal and external heat index

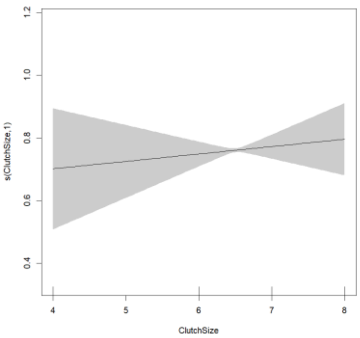
2.2 Breeding parameter graphs

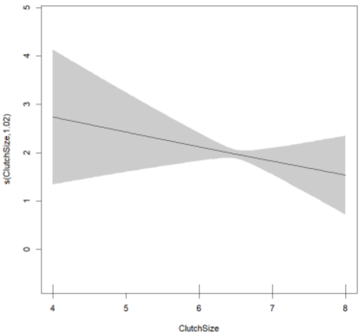
2.2.1 Clutch size

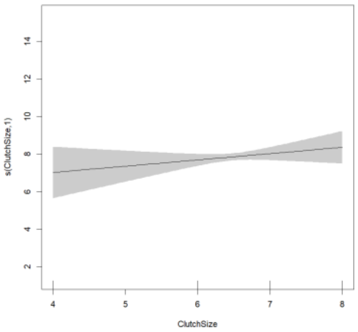
2.2.1.1 4-minute scale



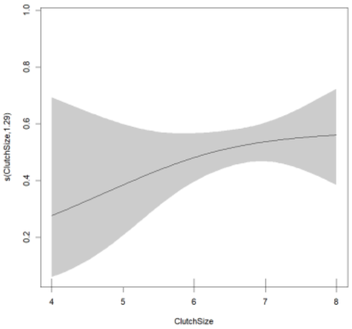
2.2.1.2 Hour scale

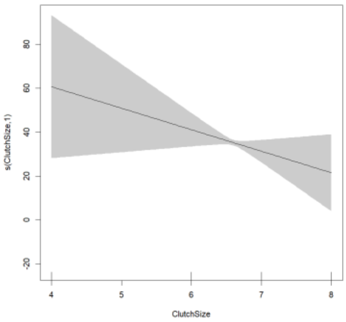


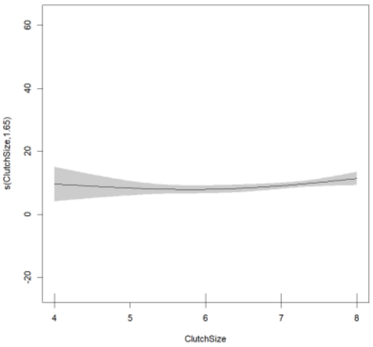




2.2.1.3 Day scale

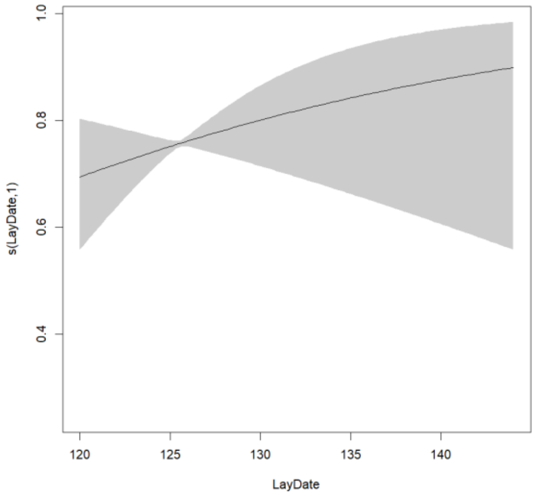




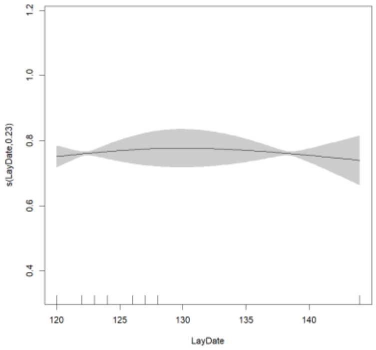


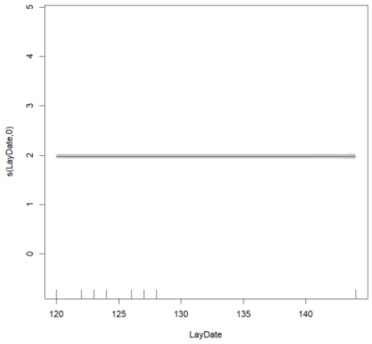
2.2.2 Lay date

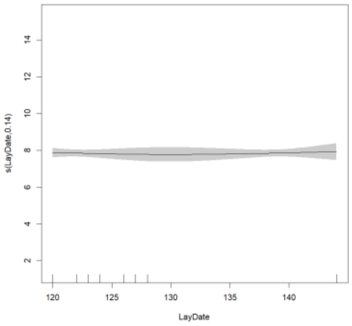
2.2.2.1 4-minute scale



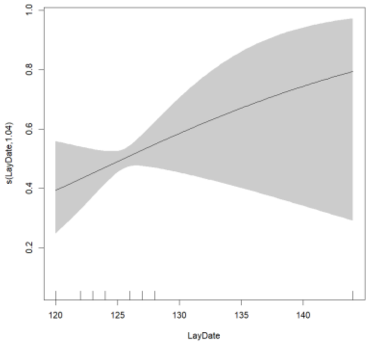
2.2.2.2 Hour scale

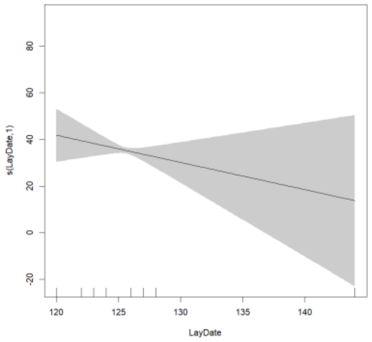


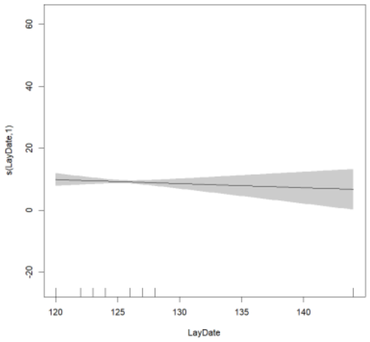




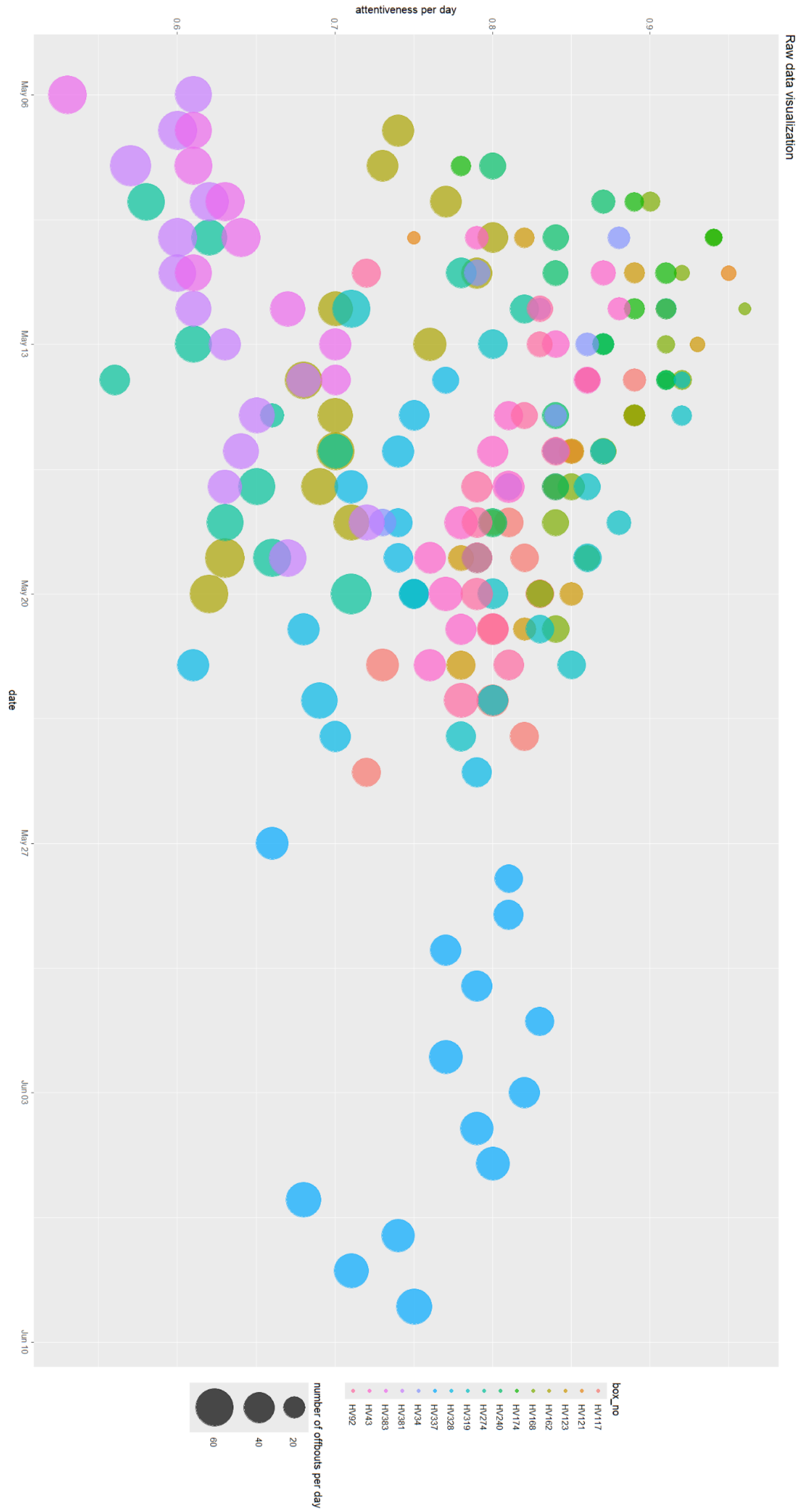
2.2.2.3 Daily scale







2.3 Raw data scatter


Raw data visualization
attentiveness per day
0.6
0.7
0.8
0.9
date
May 06
May 13
May 20
May 27
Jun 03
Jun 10
box_no
HV117
HV121
HV123
HV162
HV168
HV174
HV240
HV274
HV319
HV328
HV337
HV34
HV381
HV383
HV43
HV92
number of offbouts per day
20
40
60