Agricultural land use and reproductive behaviour constrain responses to summer thermal stress in a large herbivore

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Abstract

Agricultural land use and climate change are major global threats to terrestrial biodiversity. However, their interactive effects on synanthropic species are only recently being addressed. Behavioural plasticity is the most likely candidate mechanism for coping with rapid environmental change, yet behavioural adjustments may be insufficient when multiple anthropogenic pressures, such as human land-use and rising temperatures, coincide with strong life-history constraints. We investigated how agricultural land use shaped the availability of thermal refuge and mediated responses to high temperatures during the mating season in roe deer (*Capreolus capreolus*), a large herbivore present in most European agricultural landscapes. We demonstrated that woodland provided more efficient thermal refuge than anthropogenic vegetation such as hedges or tall crops. The combination of high temperatures, agricultural land-use and reproductive constraints were dealt with differently by males and females. Females adjusted their habitat use and activity patterns to limit exposure to high temperatures, causing a greater loss in the availability of efficient cover habitat for females with little access to woodland. Males, however, did not modify their habitat use, but strongly decreased activity and distance travelled on hot days, probably due to strong reproductive constraints. We show that the extent to which behavioural plasticity mitigates the effects of high temperatures is context-dependent and may not always suffice in anthropized landscapes where thermal buffering habitats are rare. Restoring woodland patches and hedges, while considering how climate change modifies the use of substitute habitats shaped by human activities, will be key in promoting species' resilience within agricultural areas.

Key words: Anthropogenic effects, Climate change, Agriculture, Temperature, Behavioural plasticity, Ungulate, Reproduction

Introduction

Rapid climate change is challenging the persistence of species inhabiting anthropogenic landscapes (1, 2). Cities, for example, are predicted to experience drastic changes in species communities as global temperatures increase (3, 4), potentially driving the loss or replacement of species that had successfully adjusted to urban environments (5, 6). The persistence of species under climate change in less artificial but, nevertheless, clearly anthropized areas such as agricultural landscapes, has attracted less attention and has only recently been studied, mostly at large scales (7–10). Agricultural landscapes are expected to become warmer and drier than more natural habitats (11), mostly because of the structural homogeneity of crops and the general lack of canopy cover to provide thermal-buffering

(12). Recent studies reported that the conversion of tropical forests to open agricultural fields led to more than 10°C differences in local temperature compared to intact, more shaded areas (13). Because novel climatic constraints are often exacerbated in human-altered habitats, populations that must already cope with a variety of anthropogenic pressures may thus be put in even greater jeopardy (14). As global change accelerates, we urgently require a better understanding of how synanthropic populations can rapidly cope with these multiple sources of stress, especially through behavioural plasticity.

Behavioural adjustments to high temperatures are often constrained by a combination of factors, notably the availability of thermal refuge (15), predation risk (16), and life history constraints linked to reproductive status, age and sex (17). These behavioural trade-offs are expected to be particularly acute during periods when energetic demands are high. For instance, when temperatures were very low during the reproductive period, lactating female bats (*Myotis daubentonii*) spent less time in torpor than males to maintain resource allocation to juveniles (18). Similarly, Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) females with lambs selected less risky habitats than males during the summer but, by doing so, exposed themselves to higher temperatures (19). Species that reproduce during periods of high temperatures in habitats with low thermal buffering capacity may then face a "perfect storm" scenario (20), in which environmental and internal constraints combine to ultimately limit population viability (11, 14).

Large mammals are expected to escape heat by seeking shade and using cooler, often thermally more stable, microclimates when solar radiation and air temperatures rise (15, 17). Specifically, in response to high temperatures, many desert, tropical and cold-adapted large mammals are known to modify their habitat preferences by selecting for canopy cover (such as forests) or cooler, wind-exposed areas (moose (*Alces alces*): 21-22, African ungulates: 23, mouflon: 19, giant anteater (*Myrmecophaga tridactyla*): 24). Some species also adjust their daily activity patterns when temperatures rise, reducing activity during the hottest hours of the day, and increasing activity during the coolest periods (16, 21–23). Various studies have investigated the behavioural responses of large mammals to high temperatures in tropical, desert and cold-adapted species in protected or natural habitats (19, 24–28). However, to our knowledge, none have evaluated the behavioural responses of individuals to the combined effects of high temperatures and agricultural land-use in large mammals (but see: 24).

Understanding how synanthropic species adjust their behaviour to high temperatures is crucial to guide management and conservation practices in agricultural areas (that represented 33.8% of Europe's land surface in 2020, 29), especially for species that reproduce when temperatures are at their peak. Here, we investigated how variation in the availability of thermal refuge in agricultural landscapes shaped the behavioural responses of European roe deer (*Capreolus capreolus*) to high temperatures during the mating season, using 12-years of GPS-tracking and activity data from 154 GPS-monitored individuals. Roe deer have been present in most European agricultural landscapes since the second half of the 20th century (30), yet their persistence may be challenged in the upcoming years as they occur at only very low densities in biomes with high temperatures and low precipitation levels (31). Furthermore, they are one of the few large herbivores that mate during the height of the summer due to a five-month embryonic diapause (32), so that adult males must maintain high activity levels during summer as they are strictly territorial (33) and allocate intensively to territorial and mating behaviours. We, therefore, expected that roe deer would respond strongly to variations in thermal conditions determined both by ambient temperature and the thermal-buffering characteristics of the habitats they use, and that these responses would be mediated by the agricultural context of their home range and sex.

Given this context, we tested (i) if natural shaded habitats, such as woodland, offered higher thermal buffering capacities than more anthropogenic wooded habitats, such as hedges, and crops, such as maize, (ii) if, as temperature increased during the hottest hours of the day, individuals changed their space use in favour of habitats providing efficient thermal refuge, and modified their activity rhythm in favour of nocturnal and crepuscular periods on hot days, (iii) if individuals with less woodland in their home range – i.e. those living in a more agricultural context - responded more acutely to higher temperatures than individuals with more available woodland (iv) if males and females adopted different responses to high temperatures, with males being less plastic in their habitat use and activity patterns than females due to their territorial and mating behaviours.

Materials and methods

Study site and population

We studied roe deer living in a 19 000-ha rural region in the Vallons et Coteaux de Gascogne area, in southwestern France (Zone Atelier PyGar; N43°17, E0°53). The region is characterised by a mild oceanic climate, with annual mean temperatures around 13°C (mean 12.8°C ± SD 1.37) and annual precipitation around 600mm (609mm ± 191). Summer temperatures have consistently risen in the past decades, with an overall 0.4°C increase recorded between 1950 and 2012 in the study region and a gradual rise in maximum daily temperatures since 1975 ((34), Figure S1 source: Météo-France). Climatic models for the near future (2021-2050) predict a 1.3°C increase in mean summer temperatures, with 6 days of extreme heat in summer (daily maximum temperature >35°C) for a typical year (35). In 2022, local weather stations recorded 8 days with daily maximum temperature >35°C on our study site. Trophy hunting (targeting males) and drive hunting of other species (wild boar, fox) occur from June to September, with regular human disturbance due to agricultural activities. This likely maintains a high perception of risk for roe deer during the summer, as human activity is the main source of mortality and disturbance for roe deer in the area (36). This period overlaps with the rut season (37), when male activity generally strongly increases in July and August in this population (38). The density for this roe deer population was estimated around 8 individuals/100 ha using capture-mark-recapture re-sighting (39).

Landscape composition and shaded habitats

The landscape is a heterogeneous agricultural mosaic composed of crops (38.9%), natural meadows (28.7%), woodland (18.9%, two main forests and fragmented woodland patches) and hedgerows (3.5%), interspersed with a network of roads connecting isolated houses, farms and small villages. We focused on three land cover types, woodland, hedges and maize (a common crop that is still standing during summer on this site, representing 27 ± 6% (mean ± SD) of all summer crop surfaces across years), that were susceptible to provide sufficient shade on hot days and are known to be selected for vegetation cover during daytime in summer by roe deer (40). We mapped the distribution of each land cover type using manually digitized and homogeneous habitat patches (in ArcView GIS 3.3, Esri, Redlands, CA, U.S.A.) based on aerial photographs of the study site (from the IGN’s BD Ortho, http://professionnels.ign.fr/bdortho-50cm) and confirmed by annual field observations.

Roe deer biologging data

We measured roe deer habitat use using GPS data collected on 154 individual roe deer (108 reproductive females and 46 adult males) from 2011 to 2022, with a 1h fix rate during summer (Lotek and Vectronic collars, see Appendix S1.1 for details). Female roe deer first come into oestrous during their second summer (ca. 15 months of age), whereas males only exhibit consistent territorial behaviour during their fourth summer (i.e. at 3 years of age), although some two-year-olds males may be sexually active and successfully reproduce (33). We then analysed data for adult females aged at least 15 months old in summer and adult males aged at least 2 years old in summer. All GPS collars carried an activity sensor which indexed intensity of movement on the x (forward-backward) and y (sideways) axes every 5min (see Appendix S1.1 and Appendix S1 of (40) for a technical description). We measured total activity as the sum of activity values for both axes (range 0-510). All capture and marking procedures were done in accordance with local and European animal welfare laws (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

Local weather data

We obtained hourly measures of ambient temperature and solar radiation, from July 1st to August 31st, from a local weather station located on our study site (except for 2020 which was taken station from the weather station from the Observatoire Spatial Régional (CNRS/INSU) within 50km of our study site, see Appendix S1.2 for details). We used these data to determine which hours of the day were potentially the most constraining for roe deer in terms of thermal stress, i.e., with the highest solar radiation and highest ambient temperature ((15), see Figure S1) at the landscape level.

Variation in temperature among shaded habitats

We first evaluated whether different habitats providing shade (hereafter 'shaded habitats') had similar daytime air temperatures (hereafter temperature) and if woodland buffered daily variations in temperature more than other shaded habitats. We compared the variations in temperature across the 24h-day cycle in woodland, hedges, and maize. We measured temperature continuously over the 2023 summer season using thermologgers (TOMST, https://tomst.com/web/en/systems/tms/thermometer/). We placed four thermologgers in each land cover type across the study site, encompassing the main areas in which roe deer were captured (Figure S2), and programmed them to record temperature every 15 minutes from July 1st to August 22nd, 2023. Thermologgers were equipped with sun shields and positioned at 80-105cm from the ground to approximate temperatures at the height of a standing roe deer (Figure S2). The temperatures recorded at the station were highly correlated with those recorded directly at the study site by the thermologgers during this short-term monitoring period (Figure S3).

Habitat use under high ambient temperatures

We investigated how high ambient temperatures (recorded at the weather station) and woodland availability affected the use of woodland, hedges and maize. Indeed, roe deer are known to select woodland as refuge habitat against predation and disturbance during daytime (41) and to substitute woodland with hedges or maize, when the former is scarce (40, 42). As our field measures confirmed that woodland acted as a thermal buffer habitat (shaded and cooler) when temperatures increased (see Results), we expected that the use of woodland, hedges and maize would depend on the availability of woodland in the local landscape, as thermal refuge may be a limiting resource under high temperatures. We therefore expected that the use of woodland, hedges and maize would increase more strongly for individuals with low woodland availability, if these habitats were used as thermal refuge.

As we were interested in the fine-scale responses of individuals to heat, we focused on locations during the hours with the highest mean temperatures and solar radiation measured at the weather station during summer (15). We identified 2pm (14h) local time (i.e., 12pm UTC) as one of the hours of the day with the highest mean temperature and solar radiation (Figure S1). We also observed that 2pm was the hour of the day at which the difference in temperature among habitats was greatest (Figure 1); hence, we focused the analyses on this hour. We defined habitat availability as the proportion of a given habitat in the individual's 95% summer home range (June-August), using the fixed kernel method at 95% with an ad hoc smoothing parameter (43). Availability of woodland was strongly negatively correlated with the availability of agricultural land (comprising summer crops, spring crops and meadows: Pearson correlation coefficient = -0.87) and moderately with the availability of hedges (-0.57). Low woodland availability is therefore generally associated with high proportions of agricultural land and hedges within the home range.

For each habitat, we fitted a generalized linear mixed model (GLMM) with a logit link function, considering habitat use at 2pm as a binary response variable (presence in the focal habitat vs. presence in another habitat), and temperature at 2pm, woodland availability and sex as fixed effects. We included the three-way interaction as we were interested in how woodland availability could shape roe deer habitat use when temperatures increased and whether these responses differed between sexes. When fitting models for hedges or maize use, we likewise controlled for, respectively, hedge and maize availability, by including them as fixed effects. We logit transformed all habitat availability metrics to maintain linearity on the logit scale (following 42; 44; 40). We included individual identity as a random intercept to control for repeated observations. For these analyses, we only considered individuals that were monitored for ≥15 days and had more than 1% of the focal habitat and less than 99% of woodland in their summer home range to ensure that we could compare patterns of habitat use across a gradient of home range compositions.

Daily activity patterns under high temperatures

We tested whether male and female roe deer modified their daily activity patterns in response to high temperatures and if these changes in activity patterns depended on the availability of woodland in their home range. We first classified activity sensor data into 'active' versus 'inactive' behaviour using Hidden Markov Models (HMMs). HMMs can classify telemetry data into latent behavioural 'states' given the distribution of the movement or activity metrics associated with each point (45). For each individual, we then fit an HMM on the activity data recorded by the GPS collars (every 5min) from 1st July to 31st August and classified each activity value as either 'active' or 'inactive'. Visual inspection confirmed that these classifications were biologically meaningful (Figure S5).

We then compared the proportion of time an individual was active during four periods of the day (daytime, night-time, dawn and dusk) according to sex, maximum temperature for that day and woodland availability. We defined the proportion of time spent active as the proportion of activity measures classified as 'active' for each individual-day-period. We determined sunset and sunrise for each day using the 'suncalc' package (46) and defined dawn and dusk as two-hour periods, centred on, respectively, sunrise and sunset. We differentiated dawn and dusk in our analyses as temperatures are generally higher during dusk and could thus impose a higher constraint on activity.

For each period of the day (daytime, night-time, dawn and dusk), we fit a generalized additive mixed model (GAMM) with a binomial distribution and a logit link function using the proportion of time spent active as the response variable and daily maximum temperature, woodland availability and sex as fixed effects. We included the three-way interaction as we wanted to test whether females and males adjusted the timing of their activity bouts differently in relation to daily temperature and to the amount of available woodland. We fit a sex-dependent penalized spline on day of the year to account for seasonal differences in activity levels linked to the rut season, especially for males (38, Figure S6-7). We added individual identity as a random intercept to account for repeated observations. Finally, as we wanted to test whether the observed changes in activity rhythms had consequences for the total time spent active during a 24h-day cycle, we ran the same model on the time spent active across the 24h-day cycle.

Constraints of high ambient temperatures and woodland availability on territorial and mating behaviours of males

We then investigated whether the space use and activity patterns we observed for adult males under high temperatures constrained their behaviour during the rut. As adult males must patrol their territory daily during the rut to chase off other males and to encounter receptive females (37), an increase in daily distance travelled (DDT) appears to reflect allocation to reproductive behaviours in male roe deer (38).

We therefore tested whether DDT was affected by maximum daily temperature and woodland availability. Following Malagnino et *al.* (38), we calculated the mean linear distance between consecutive 1h GPS locations (or 'step lengths') over a 24h-day period for each individual-day and multiplied it by 24 to obtain an estimate of DDT over a 24h period. Although this method underestimated real daily travelled distances due to the rather low GPS fix rate (47), we considered this proxy to be biologically meaningful as we compared relative differences in DDT across individual-days with the same GPS location acquisition schedule. We restricted our analyses to individual-days with at least 22 locations (92% over 24h) to ensure that DDT was comparable across individual-days. We then fit a GAMM with a gaussian distribution for errors, setting log-transformed DDT as the response variable and maximum daily temperature, sex, and woodland availability as fixed effects. We included the three-way interaction as we expected different responses between males and females in relation to both woodland availability and temperature due to male reproductive behaviours. We controlled for seasonal and sex-specific variation in movement rates, due to rutting behaviour, by including a sex-dependent spline on day of the year (Figure S7). As before, we accounted for repeated observations by including a random intercept for individual identity.

Interpreting model predictions

For each model, we performed contrast analyses between daily maximum temperatures of 20°C and 35°C and between woodland availability of 10% and 40%. These values were chosen as they were close to, respectively, the 1st and 3rd quartiles of the distribution of these variables in our dataset. We used Mean Square Error (MSE, also known as Brier's Score when calculated for binomial models), to assess goodness of fit as it can be used across model types and rather intuitively measures how far the model predictions are from the initial observed values (48). Low MSE values indicate high goodness of fit, but MSE must be interpreted in the units and scale of the response variable. Analyses were performed in R version 4.0.2 (*R Core Team* 2019 (49)) with packages detailed in Appendix S1.3.

Results

Thermal heterogeneity in shaded habitats

Mean temperatures recorded by thermologgers during summer of 2023 differed across shaded habitats (Figure 1). We found that temperatures were systematically lower during daytime and varied less across the 24h cycle in woodland than in hedges or maize fields. Discrepancies between habitats were strongest at the hottest hours of the day (Figure 1), with temperatures recorded at 2pm in maize, on average, 3°C higher than in woodland. Woodland buffered the increase in overall temperature better than hedges, and hedges provided lower temperatures than maize when ambient temperature increased (Figure S3).

Habitat use in response to high ambient temperature and woodland availability

MSE scores for each model fit were 0.15, 0.10 and, 0.08 for the woodland, hedges, and maize use models, respectively. Therefore, our models explained a large part of the variation in the data, as the average error between the observed proportions of use for each habitat and those predicted by the models was low ($MSE<0.16$, for observed proportions ranging from 0 to 1).

Female roe deer changed their habitat use in response to high temperatures at 2pm, but this response varied in relation to the availability of woodland in their home range (Figure

2, Table S1). As expected, females with 10% woodland in their home range used woodland and hedges more as temperatures at 2pm increased (Table S2, at 35°C vs. 20°C: woodland: odds ratio=2.01, t ratio= 4.36, $P<0.001$, hedges: odds ratio=1.56, t ratio= 3.25, $P<0.03$). They drastically decreased their use of maize under higher temperatures, being nearly three times less likely to use maize as temperature increased from 20°C to 35°C (Table S2, 35°C vs. 20°C: odds ratio=0.355, t ratio= -4.61, $P<0.001$). The response of females with a higher availability of woodland (40%) was less marked, as they generally used woodland more often (Table S2, 10% vs. 40%: odds ratios<0.15, t ratios<-10, $P<0.001$) and hedges two to three times less, regardless of temperature (Table S2, 10% vs. 40%: odds ratios>2, t ratios>3.5, $P<0.01$). The interactive effect of woodland availability and temperature was not significant in the model for hedge use, although visual inspection of the predictions suggested that the effect of temperature might depend to some degree on hedge availability (predictions are for mean hedge availability=0.03 in Figure 2, Table S1).

Male roe deer did not change their habitat use in response to temperature (Table S2, 35°C vs. 20°C: all absolute value |t ratio| < 2.2, all $P>0.3$). Males with more woodland in their home range systematically used woodland more, and tended to use hedges less, than individuals whose home ranges had less woodland (i.e., with more crops and hedges, Figure 2, Table S2).

Circadian activity rhythms on hot days

MSE for each model fit were 0.009, 0.010, 0.038, 0.030 for the models of daytime, night-time, dawn and dusk activity respectively. Therefore, our models explained a large amount of the variation in the data, as the average error between the observed values for the proportion of activity during each period of the day and those predicted by the model was low (MSE<0.04).

We found strong responses of daily activity levels of both sexes to high ambient temperature and woodland availability (Figure 3, Table S3). Females shifted their circadian rhythm on hot days, lowering their activity during daytime by 12-15% as temperature increased from 20 to 35°C (Table S4, 35°C vs. 20°C: all odds ratio<0.89, t ratio< -12.7, P<0.001) and increasing their activity at night-time, dawn and dusk from 14% to 29% (Table S4, 35°C vs. 20°C: all odds ratio>1.14, |t ratio|> 5.8, P<0.001). Males drastically decreased their activity during daytime across this same temperature range, with up to 45% less of their time spent active (Table S4, 35°C vs. 20°C: all odds ratio<0.67, t ratio> 26, P<0.001), but only males with low woodland availability seemed to partially compensate for this loss during the night-time and at dawn by increasing activity slightly (Table S4, 35°C vs. 20°C: all odds ratio>1.07, t ratio >3.1, P<0.01). Females with more woodland in their home range were systematically more active during daytime (Figure 3, Table S4, 10% vs. 40%: all odds ratio<0.88, t ratio<-3.1, P<0.04), whereas males with more woodland in their home-range were systematically less active at night-time (Figure 3, Table S4, 10% vs. 40%: all odds ratio>1.19, t ratio>3.1, P<0.05).

Potential constraints of thermal stress on reproductive behaviour in male roe deer

MSE for the model predicting the probability of activity over the 24h cycle was 0.004. MSE for the model predicting DDT was 0.79, indicating that the model goodness-of-fit was quite low, as differences between the predicted and observed values diverged, on average, by around 0.8km. This must be considered in the light of the very high variation observed amongst DDT values (ranging from 0.15 to 11km) but calls for caution in the interpretation of these results.

Male roe deer showed a net decrease in both total activity (across the 24h cycle) and predicted DDT as daily temperatures increased (Figure 4). Males decreased their total activity over the 24h cycle by 17-23% when the temperature reached 35°C, compared to when it was 20°C (Table S6, 35°C vs. 20°C: all odds ratio<0.86, t ratio<-15, P<0.001) and this decrease was stronger for males with more woodland in their home range (Table S6). In contrast, female activity and mean DDT was not affected by daily temperatures (Tables S5-S6). Females with greater woodland availability maintained higher activity levels across all temperatures in comparison to females living in more agricultural contexts (Table S6, 10% vs. 40%: all odds ratio<0.92, t ratio<-3.1, P<0.055).

Discussion

Agricultural land conversion and climate change are widely identified as major global threats to terrestrial biodiversity (50), yet their interactive effects on synanthropic species have only recently been studied, mostly with a particular focus on population responses at large spatial scales (2, 8–10). Our study is one of the few to consider the interactive effects of high temperatures and agricultural land-use on a synanthropic large mammal from a behavioural perspective and the first to test how individual traits (sex) and life history phenology (reproductive timing) influence these responses. We show that the extent to which behavioural plasticity mitigates the effects of high temperatures is context-dependent and may not always suffice in anthropized landscapes where habitats that provide thermal refuge are rare.

We found that agricultural land-use shaped the availability of cooler, shaded habitats for roe deer. Agricultural habitats were characterised by a lower proportion of woodland and a higher proportion of hedges and summer crops, such as maize, which provided hotter conditions during daytime, and did not buffer the increase in ambient temperature, compared to woodland. We observed up to 3°C differences at 2pm between maize and woodland, corroborating recent analyses reporting global mean differences of 1.7°C in mean and 4.1°C in maximum temperatures between forest and open-field conditions (51). Hedges were systematically warmer than woodland during daytime, underlining the fact that canopy surface, structure, and understory density are particularly important in creating microclimates that effectively buffer temperature extremes (52, 53). Maintaining or restoring forest patches alongside the plantation of hedges within agricultural areas may then have strong impacts on the availability of thermal refugia and possibly buffer the impacts of high temperatures on wildlife living in agricultural landscapes.

A key finding of our study was that the behavioural responses of female roe deer to high temperatures were mediated by woodland availability. Female roe deer with little woodland in their home range strongly increased their use of woodland and, to some extent hedges at 2pm when temperatures were high, but almost completely ceased to use maize, even though maize generally serves as substitute cover habitat during daytime when woodland and hedges are scarce (40). Similar behavioural plasticity in an agricultural landscape was observed for giant anteaters living in an extensive cattle ranch in Brazil: individuals selected for woodland over open crop areas during daytime only when temperatures were high (26). Here, we showed that high temperatures interacted with agricultural land-use to redefine habitat quality at the individual level, resulting in a net loss in the availability of habitat providing cover for females that had switched to using tall crops to compensate for a lack of more “natural” canopy cover in their home range. Similarly, recent studies revealed that nest-boxes deployed for the conservation of arboreal marsupials in Australia, where natural dens were destroyed by human activities, did not buffer high temperatures (54) and resulted in lower nest-box occupancy during summer (55). Considering how high temperatures alter the use of substitute habitats created, directly or indirectly, by human activities, is then crucial to better predict and mitigate the effects of rising temperatures on wildlife.

Behavioural adjustments in response to high ambient temperatures to limit thermal stress may not always be possible due to life history constraints. In contrast to females, we found that the habitat use of male adults during summer was not influenced by high temperatures. We suggest that territoriality constrained the spatial responses to heat, as territorial males must patrol the same area to conserve their territory, even where woodland availability is low. Preliminary observations indeed revealed that yearling males, who are often non-territorial and excluded from male adult territories (33), responded in the same way as females, abandoning maize for woodland and hedges when temperatures were high (unpublished results). As roe deer either maintained (male adults) or increased (female adults, yearling males) their use of woodland and hedges when temperatures increased, social interactions between the sexes and age classes likely also increase during hot weather ('clumping' effect, (56)), especially if woodland is concentrated in small and isolated patches. For instance, social interactions were influenced by high air temperatures for zebra finches (*Taeniopygia guttata*) in an arid Australian zone, as group foraging at feeders strongly decreased at high temperatures (57). Further work should evaluate if high temperatures modify social interactions, possibly creating greater spatial or temporal overlap between individuals in territorial systems where thermal refuges are heterogeneously distributed in the landscape.

High temperatures and agricultural land use combined to compress the spatiotemporal niche of roe deer (sensu (58)), by restricting both the habitats that could be used during daytime at the height of summer, and the time available to fulfil their daily requirements. Both male and female roe deer strongly reduced their diurnal activity on hot days, but only females compensated for this loss by increasing their nocturnal and crepuscular activity. During summer, females mostly allocate time to foraging, while males increase the time allocated to territorial and mating behaviours (56, 59). Although shifting to nocturnal activity may reduce energetic losses due to thermoregulation (60), our results suggest that this resulted in females condensing their activity within a shorter time period and males reducing their total activity over the 24h diel cycle. We also found that females with less woodland in their home range consistently maintained lower activity levels, both during the daytime and over the 24h cycle. Exploratory analyses revealed that activity levels of roe deer females during the daytime were higher in woodland than in hedges, except at high temperatures, and that activity in maize strongly decreased with rising temperatures (Figure S8). Higher risk perception due to hunting and human agricultural activities during daytime, dusk and dawn (61) thus seems to combine with the effects of high temperature to further constrain the activity levels of roe deer during summer in human-dominated landscapes. This aligns with a recent study across the U.S.A by Tourani et al. (9) which reported that the probability of occupancy of cathemeral-diurnal mammals decreased more strongly in human modified landscapes than in more ‘natural’ areas when temperatures increased. Considering the diel time axis as an ecological dimension, in addition to habitat and risk perception, may improve predictions on how species living in anthropogenic areas will balance their time budgets in response to rising temperatures (60), especially in contexts where circadian compensation between daytime and night-time is more difficult to achieve.

Finally, we found that reproductive males were more acutely impacted by high temperatures than females, with a much more marked decrease in diurnal activity, which they were unable to compensate for across the 24h cycle. As a result, they experienced a strong net loss in both total activity and in the total distance travelled on hot days. Since body mass dimorphism is low in roe deer, we argue that reproductive constraints may explain the differences we observed. During the rut, to maximise mating success, male roe deer perform many energetically demanding behaviours such as patrolling their territory, scent marking, parading, chasing off and fighting with rival males, as well as mating with females (33, 56), many of which are likely energetically costlier at high temperatures. For instance, as standard operative temperature was increased, captive male red-winged blackbirds (*Agelaius phoenice*) reduced the frequency of territorial displays to increase their use of shelter but maintained high-value agonistic behaviours (62). High temperatures also constrained the reproductive behaviour of fiddler crabs (*Uca mjoebergi*), such that males with burrows in the shade were able to court females on the surface for longer under extreme temperatures than males in a sunny location (63). Surprisingly, high temperatures did not affect the total activity level of females over the 24h cycle in our study, suggesting that the cost of high temperatures was lower for females, likely because they maintain overall lower activity levels than males during summer. We could not quantify the consequences of these behavioural responses to high temperatures on reproductive success in males, yet the timing and intensity of thermal extremes have previously been shown to affect mating and reproductive success for both sexes (ungulate: (64) insect: (65), crustacea: (63)). Future studies could investigate how high temperatures in agricultural landscapes can alter rut behaviour, mate choice and mating success at the individual level, to understand how high temperatures and the availability of thermal refuges may affect reproductive success differently between sexes.

Roe deer are the only Artiodactyl with a 5-month embryonic diapause, so that mating occurs in the Northern hemisphere summer rather than in autumn-winter (32). This is thought to be adaptive as it enables both parturition and mating seasons to coincide with higher forage abundance and milder climatic conditions. With rising summer temperatures and more frequent drought events in Europe, species whose evolutionary history have resulted in synchrony between hot climatic conditions and reproduction will be increasingly challenged, potentially generating novel selection pressures on reproductive phenology. Accounting for reproductive behaviours and life history traits may then help to understand how synanthropic species may respond to the interactive effects of human land-use and climate change in the near future.

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Arnaud Bonnet: Investigation – data collection; Data curation. **Simon Chamaillé-Jammes:** Conceptualization; Methodology; Writing – review and editing. **Yannick Chaval:** Investigation – data collection; Data curation. **Mark Hewison:** Conceptualization; Investigation – data collection; Writing – review and editing. **Bruno Lourtet:** Investigation – data collection; Data curation. **Joël Merlet:** Investigation – data collection. **Nicolas Morellet:** Conceptualization; Methodology; Investigation – data collection; Writing – review and editing. **Noa Rigoudy:** Conceptualization; Investigation – data collection (supporting); Methodology; Formal analysis; Writing – original draft, review and editing.

Declaration of Interest statement

The authors declare no conflicts of interest.

Data availability

We confirm that, should the manuscript be accepted, the data and codes supporting the results will be archived in Zenodo.

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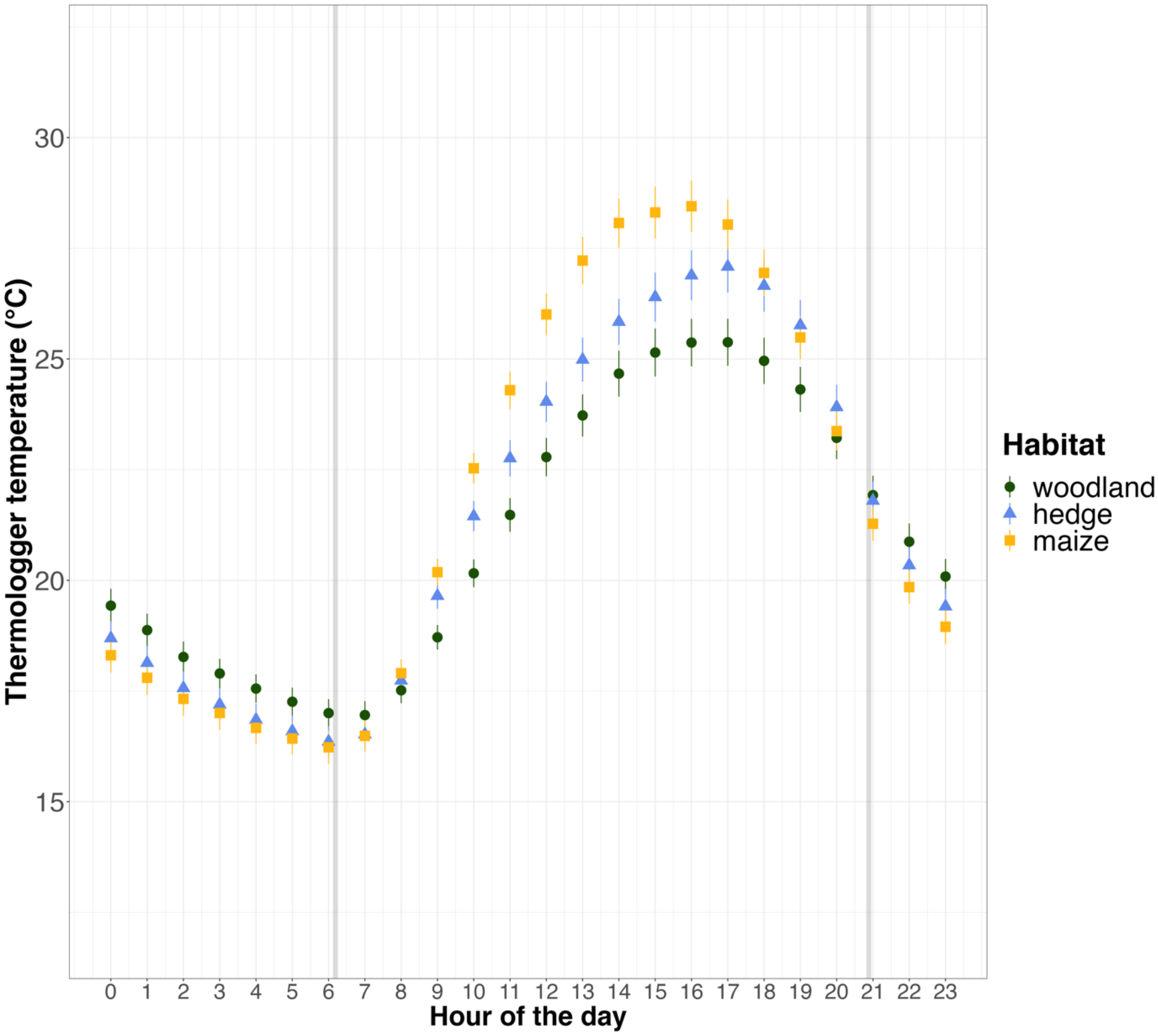

Figure 1. Variation in air temperature recorded in three habitats providing shade: woodland (dark green circle), hedges (blue triangle) and maize (yellow square), during the 2023 summer according to the hour of the day. Four thermologgers (TOMST) were positioned in each habitat across the study site, measuring air temperature continuously from July 1st to August 22nd, 2023. Points and error bars are mean air temperature ± 95% CI for each hour of the day (local time, UTC+2), with 2pm corresponding to 14h. The vertical grey bars represent mean sunrise (left) and sunset (right) hours over the summer.

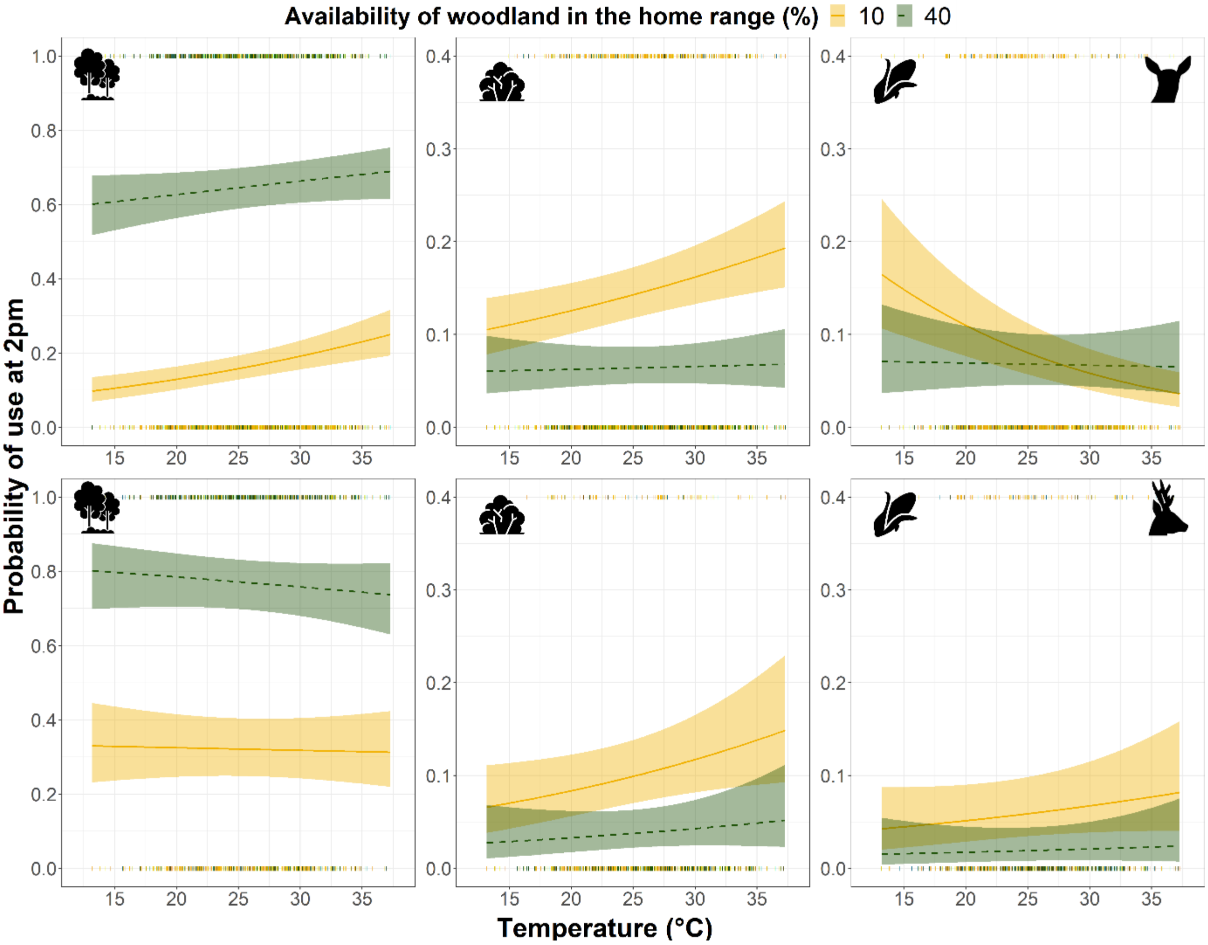

Figure 2. Predicted probability of use at 2pm (local time, UTC+2) according to air temperature and the availability of woodland in the individual's home range (10% yellow, 40% dark green and dashed) for three shaded habitats: woodland (left), hedges (centre), maize (right), for females (top) and males (bottom). Coloured lines represent mean predicted probabilities with associated 95% confidence intervals estimated using logistic regressions, controlling for respectively, mean hedge availability (0.03) and mean maize availability (0.08) in models for, respectively, hedge and maize use. Ticks represent raw data on the use (0/1) of each habitat at 2pm according to temperature and woodland availability.

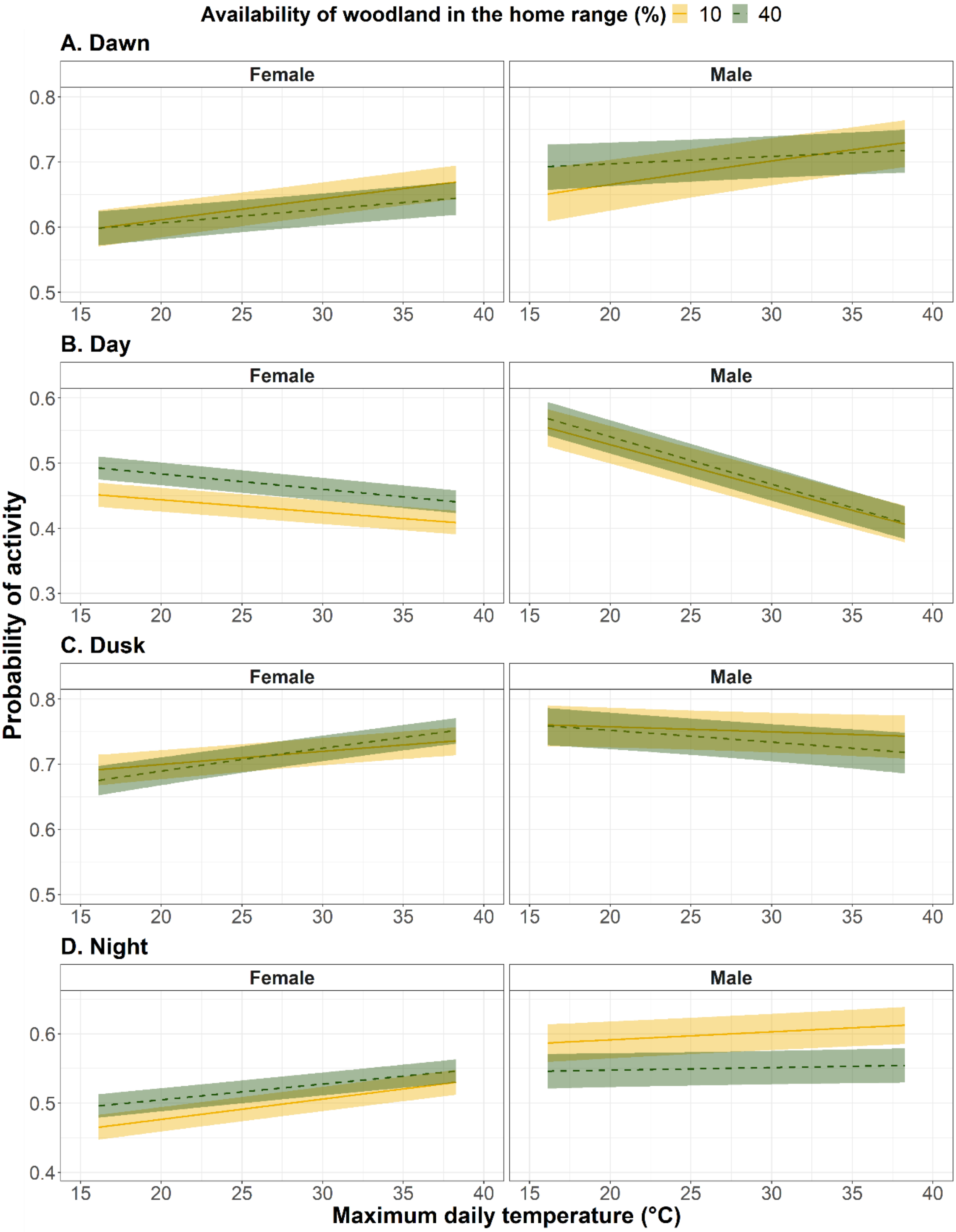

Figure 3. Predicted probability of activity according to maximum daily temperature and the availability of woodland in the individual's home range (10% in yellow full line, 40% in green dashed line) during four periods of the 24h-cycle: dawn (A.), daytime (B.), dusk (C.) and night-time (D.), for females (left) and males (right). Coloured lines represent mean predicted probabilities (fixing the day of year to 212, i.e., 31st of July) with associated 95% confidence intervals estimated using binomial generalized additive models with a logit link function.

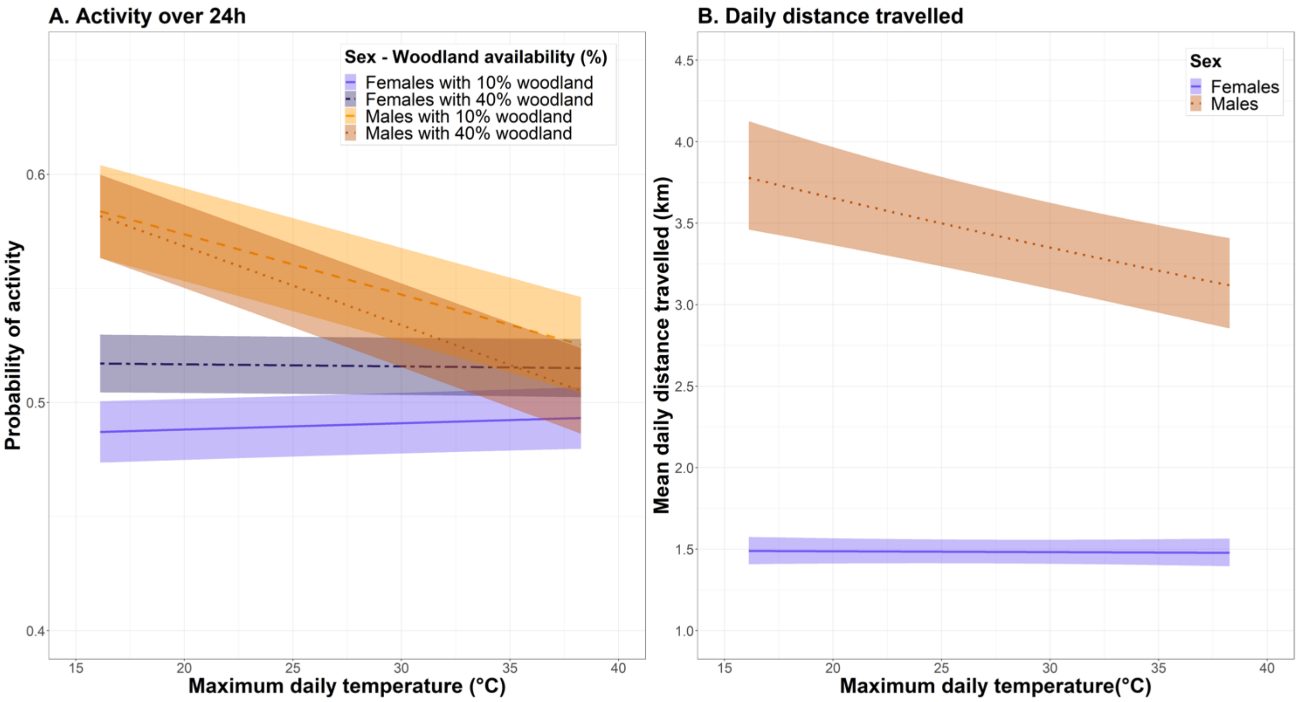

Figure 4. Overall activity level and mean distance travelled over the 24h-cycle for male and female roe deer in relation to maximum daily temperature and woodland availability. (A.) Probability of activity over the 24h cycle in relation to maximum daily temperature, sex, and woodland availability: females with 10% of woodland in their home range (light orange, full line), males with 40% of woodland (dark orange, two-dashed line), males with 10% woodland (light purple, dotted line) and females with 40% woodland (dark purple, dashed line). (B.) Mean daily distance travelled (km) as a function of maximum daily temperature for females (light purple, full line) and males (dark orange, dotted line). Coloured lines represent mean predicted probabilities with associated 95% confidence intervals (day of year fixed to 212, 31st of July) estimated by generalized additive models with binomial, respectively, or gaussian distributions for errors.