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Diel patterns of behaviour of fruit flies (Diptera: Tephritidae) in cucurbit cropping systems in Morogoro, Tanzania

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Abstract

Diel activity determines when control measures can reach cucurbit-infesting fruit flies, yet coexisting species have rarely been compared under African field conditions. We recorded roosting, feeding, oviposition and mating by *Zeugodacus cucurbitae*, *Dacus vertebratus* and *Dacus ciliatus* on three cucurbit hosts (*Citrullus lanatus*, *Cucurbita maxima* and *Cucumis sativus*) and a *Zea mays* border across four cropping seasons (2021–2022) in two agroecological zones of Morogoro, Tanzania. Roosting dominated in all three species, with maize the principal roosting site. Roosting showed species × crop and crop × daytime-period interactions, indicating species-specific crop use and diel shifts in crop use. Feeding showed a species × crop × daytime-period interaction, indicating that crop use across the day differed

among species. Oviposition showed species-specific host use, with *Z. cucurbitae* showing the clearest diel pattern, concentrated around midday. Mating was too rarely observed for factorial analysis. Site-related differences were limited, and measured weather variables provided no clear additional explanatory power after daytime period was accounted for. Overall, the species differed in how particular behaviours were distributed among crops and across the day, while strong use of non-host maize supports its further evaluation as a spatial target for behaviourally informed fruit fly management.

Keywords: *Zeugodacus cucurbitae*; *Dacus vertebratus*; *Dacus ciliatus*; roosting behaviour; non-host trap crop; oviposition host use

Introduction

Fruit flies (Diptera: Tephritidae) are pests of considerable economic importance in fruit and vegetable production globally^{1,2,3}. Damage from fruit fly oviposition and larval development⁴ ranges from 40 to 89%, depending on the host crop, location, and management practices^{4,5,6}. Generally, fruit flies can remain active throughout the year⁷, and their foraging activities on host crops may vary depending on season, crop phenology, and weather⁴.

Several programmes to manage fruit flies in cucurbitaceous crops have been developed including integrated pest management (IPM)^{8,9,10,11}. Recently, agroecological methods of pest control in cucurbit production systems have become popular. These include the establishment of trap crops to attract pests away from the main crop¹² and to offer refuges for beneficial insects¹³. Trap crops, when used as foraging and roosting sites by pests, are optimal targets for spot application of toxic baits¹⁴. Understanding diel activity patterns of fruit fly assemblages in the field can help to optimize the spot application of toxic baits in cucurbit production systems.

Circadian rhythms are categories of biological rhythms that include the rest-activity cycle^{15,16}. Organisms have evolved internal timekeepers to predict these daily changes^{17,18}. The light-dark diel cycle is the most reliable cue among environmental variables for entraining an animal's circadian system¹⁹. These circadian processes are expressed in the field as diel patterns of activity, although observations of activity across the day do not by themselves demonstrate

endogenous circadian rhythmicity. Understanding diel patterns and circadian processes that may underlie them, can help to optimize targeted application of control measures such as spot application of toxic baits²⁰. For instance, many fruit fly attractants exploit circadian-regulated foraging and mating behaviours; thus, deploying lures during periods of peak activity can increase trap catch rates²¹. Moreover, knowledge of fruit fly circadian rhythms enables optimization of pesticide application schedules and bait station placement, leading to better control outcomes and reduced pesticide use²². However, knowledge of the diel patterns of tephritid activities such as mating, oviposition, feeding and roosting is globally limited to a few species. These activities may also involve shifts in the use of host and non-host plants over the course of the day, linking diel activity with crop use within the cropping system. During host searching and oviposition, gravid females may move between non-host and host plants while searching for suitable sites to lay eggs²³.

Fruit fly activity within cucurbit fields depends on the species present, their sex, and weather conditions¹⁴. Furthermore, pest communities and their activities in agricultural fields are influenced by host crops, the surrounding environment, geographical location, natural enemies, and existing pests of similar host crops^{24,25}. Polyphagous species thrive in areas with continuous or staggered fruiting, supported by both wild and cultivated fruits^{26,27,28,29,30}. Warm, humid climates favour *Bactrocera* species, while cooler climates limit their spread^{28,31,32,33,34}. Rainfall enhances fruiting and survival of fruit flies, though extremes like drought or floods reduce their populations³⁵. Seasonal peaks of the fruit flies occur during warm, wet periods^{30,36,37}. Natural enemies help regulate numbers^{38,39}, while invasive species like *Z. cucurbitae* outcompete native species due to stronger reproductive traits^{28,32,40}. Poor practices like monoculture and lack of sanitation boost tephritid abundance, but this can be reduced through proper orchard management, including regular removal and destruction of infested fruits and elimination of alternative wild host plants around and within the fields^{28,41}.

Tanzania is an East African country with an economy largely based on agriculture. The majority of Tanzanians live in rural areas⁴² and are mostly engaged in agriculture. The horticulture industry contributes ~38% to total foreign income accrued from the agriculture sector⁴³. Tanzania has diverse climatic conditions that support the cultivation of various fruit and vegetable crops including cucurbits such as cucumber (*Cucumis sativus* Linnaeus), pumpkin (*Cucurbita maxima* Linnaeus), and watermelon (*Citrullus lanatus* (Thunb.) Mastum. & Nakai)^{36,37}. These crops are an important source of income and nutrition in the country⁴⁴ and

contribute significantly to food security and employment⁴⁵. Unfortunately, these crops are also prone to fruit fly attacks⁴⁶. Agroecology offers a promising fruit fly management system to inhibit cucurbit flies⁴¹ in Tanzania, since it is environmentally friendly and cost-effective as it reduces the reliance on agrochemical input uses^{47,48,49}. However, tephritid behavioural studies that can be used to optimize agroecological management systems have yet to be undertaken in Tanzania.

Our study aimed to investigate the diel patterns and crop use of cucurbit-infesting flies, focusing on roosting, oviposition, mating, and feeding behaviours in cucurbit crops and a trap crop under field conditions. We expected behavioural patterns to vary among species, crops and daytime periods, with species differing in their crop use and diel activity patterns. We further expected that flies would roost more frequently on maize (*Zea mays* Linnaeus)¹⁴ planted as a trap crop. This information will be useful for developing effective management strategies by determining the timing and target areas for spot application of attract-and-kill and mating disruption approaches.

Methods

Experimental setup

The studies were conducted in the Morogoro Region, Eastern Central Tanzania, from 2021 to 2022. The region has bimodal rainfall with a longer rainy season from March to May and a short rainy season from October to December⁵⁰. The region has three agroecological zones (the Plateau, Mountainous and the River basin zones). Our studies were conducted in the Plateau and Mountainous zones. The Plateau agroecological zone is located between 300 - 600 m a.s.l. and receives an average rainfall of 700 - 1200 mm per annum. The Mountainous agroecological zone is situated between 600 - 1300 m a.s.l. and receives an average rainfall of 800 mm - 2500 mm per annum⁵⁰. The annual average temperatures for both the Plateau and Mountainous zones are 18°C⁵¹. Two experimental plots were established, one in the Plateau (S06°50'58.4" E 37°39'15.5", altitude 531 m a.s.l.) and the other in the Mountainous (S06° 53' 15.9" E 37° 40' 15.5", 1 271 m a.s.l.) (Fig. 1). These sites were chosen because they are within the range of cucurbit and maize production, with similarities in agronomic characteristics. The experiments were replicated for four cropping seasons: 12 January to 10 February 2021; 5 May to 1 June

2021; 7 January to 4 February 2022; and 4 April to 2 May 2022. The methodology followed the approaches of Atiama-Nurbel et al.²³ and Deguine et al.^{1,2}.

In each agroecological zone, one experimental plot with dimensions of 45 m × 45 m was established. The plot was divided into three equal subplots (15 m × 45 m) where the following cucurbit crops were planted; cucumber (*C. sativus*), pumpkin (*C. maxima*) and watermelon (*C. lanatus*). Regardless of cucurbit species, plants were established in a grid of 1.5 m × 1.0 m in the respective sub-plots. Three rows of *Z. mays* were planted on a 1-m wide strip at a spacing of 0.3 m × 0.3 m along the borders of each cucurbit crop as a trap crop¹⁴. A space of 0.5-m wide was maintained between each sub-plot to allow movement of observers (Fig. 2). *Z. mays* was planted 30 days before the planting of the cucurbit crops. No synthetic- or biopesticides were applied to the plots. Standard agronomic practices such as weeding, watering, and fertilizer application were performed. The cucurbit species and maize trap crop occupied fixed positions within the experimental layout rather than independently randomized treatment plots.

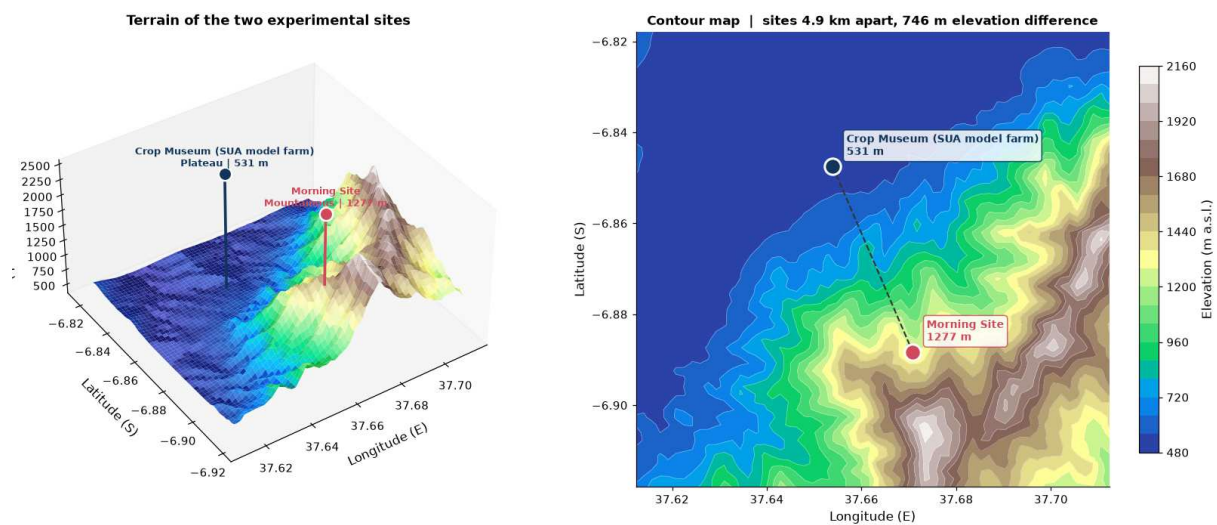


Figure 1. Altitudinal setting of the plateau and Mountainous experimental sites. SRTM 30 m elevation data (NASA/USGS) retrieved from Open Topo Data.

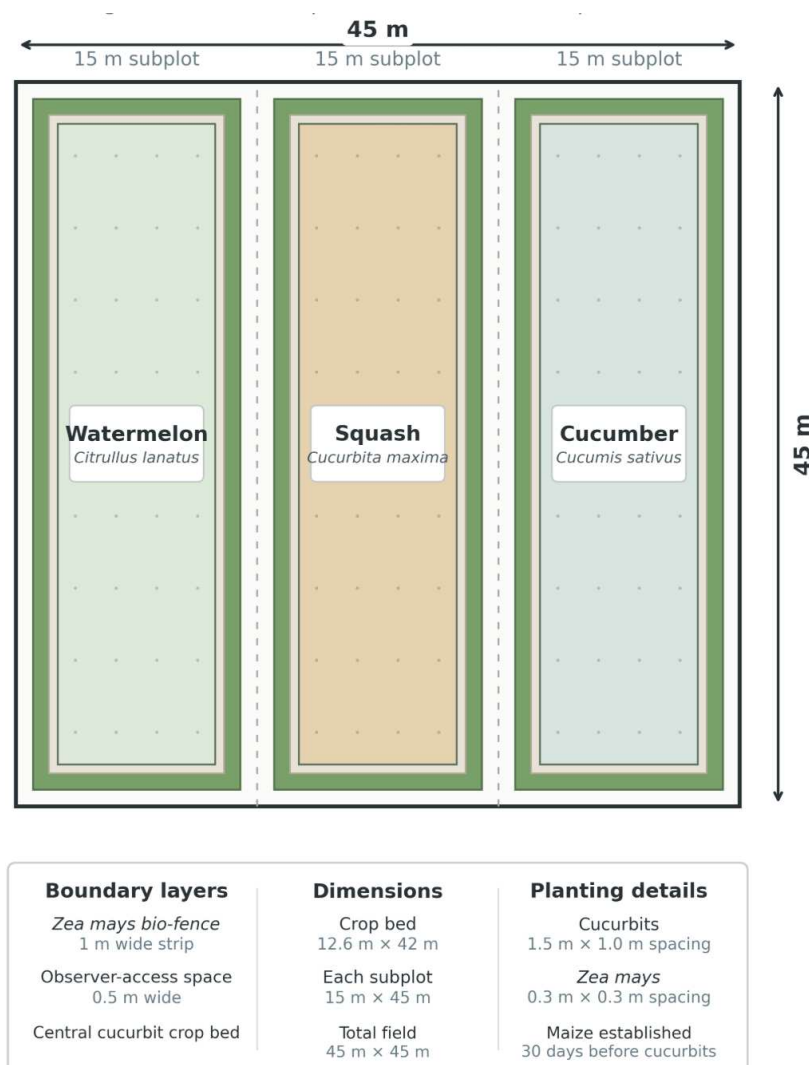


Figure 2. Layout of the experimental plots under each agroecological zone of Morogoro: The Plateau zone (Crop Museum) and Mountainous zone (Morning Site).

Behavioural observations of fruit flies in cucurbit crops and trap plant

Adult fruit flies were observed, counted and recorded when roosting, feeding, ovipositing, and mating on cucurbit crops or *Z. mays* trap crop. We recorded the behaviours patterns once per week for five consecutive weeks during each cropping season. Adult flies were recorded feeding when seen imbibing water and/or feeding on food sources such as bird droppings, nectar, and sugar substances. Mating was recorded when males mounted female flies. Oviposition was recorded when gravid females were seen drilling on host surfaces with an ovipositor to lay eggs. Roosting was recorded when flies were resting on crops without any locomotory activity.

Adult fruit flies (both males and females) were observed for 30 minutes on maize and cucurbits at a selected patch of 10-m². A patch was randomly selected each morning of on each sampling

day and marked. Observations were done five times a day between 07:00 and 18:30 as follows: 07:00–07:30 (early morning), 10:00–10:30 (late morning), 13:00–13:30 (midday), 15:00–15:30 (afternoon), and 18:00–18:30 (evening). Care was taken not to disturb the flies during the observations. Each plot was attended by four trained observers who identified species and recorded behavioural activities (mating, oviposition, feeding, and roosting) during each observation period. There was an interval of approximately two and a half hours (150 minutes) between observation periods. In the evening, the observers sometimes used light sources (a torch) to observe the flies. The observed fruit flies were identified using taxonomic features presented by⁵². Some morphological features of the flies were printed on A4 cards to aid quick identification. Hand lenses were also used to support observations. Some specimens were periodically collected using sweep nets to confirm identification in the laboratory. Counts of each behavioural activity were recorded for each fruit fly species, crop and daytime period and retained on their original scale for statistical analysis.

Data analysis

Counts recorded for each species, crop, and 30-min observation were analysed on their original scale. Repeated observations from the same site and date formed 40 sites $\times$ date clusters (2,400 records). The two sites were treated as field blocks/replicates; because site, elevation, and agroecological zone were aliased, no separate site or elevation effect was inferred. crop locations were fixed, so crop contrasts are associations within the study system. Mating (21 events) was summarized descriptively.

Roosting, feeding, and oviposition were analysed separately using population-averaged negative-binomial generalized estimating equations with log links, exchangeable within-cluster correlation, and bias-reduced sandwich covariance estimates^{53,54,55}. Models included species, crop, daytime period, sampling season, and site as a blocking factor. Oviposition models were restricted to the three cucurbit crops. Primary screens tested main effects and one estimable two-way interaction at a time; false-discovery rate was controlled with Benjamini–Hochberg adjustment⁵⁶. Pairwise adjusted-mean ratios have pointwise 95% delta-method confidence intervals, with Holm-adjusted P values⁵⁷. The categorical feeding crop $\times$ period and three-way feeding models were non-estimable; the reduced maize-versus-pooled-cucurbit continuous-time model is exploratory. Similarity among species in proportional crop-position and daytime-period use was summarized descriptively using pairwise Pianka overlap indices.

Weather models considered temperature, vapour-pressure deficit, radiation, wind speed, and antecedent 3-h rainfall; relative humidity was descriptive only. Hourly ERA5-Seamless data were retrieved through Open-Meteo^{58,59}. Analyses used Python with pandas, NumPy, SciPy, statsmodels, Patsy, and Matplotlib; package versions are retained in the executable notebook^{60,61,62,63,64}.

Results

Behavioural composition and diel activity patterns

Recorded behavioural events were distributed unequally across crops (Fig. 3). Maize accounted for the largest share of events in all three species: 62.4% for *Z. cucurbitae*, 73.4% for *D. vertebratus*, and 74.3% for *D. ciliatus*. Among the cucurbit crops, *Z. cucurbitae* was most frequently recorded on *C. sativus*, whereas *D. vertebratus* had similar proportions across the three cucurbits and *D. ciliatus* was most frequently recorded on *C. maxima*.

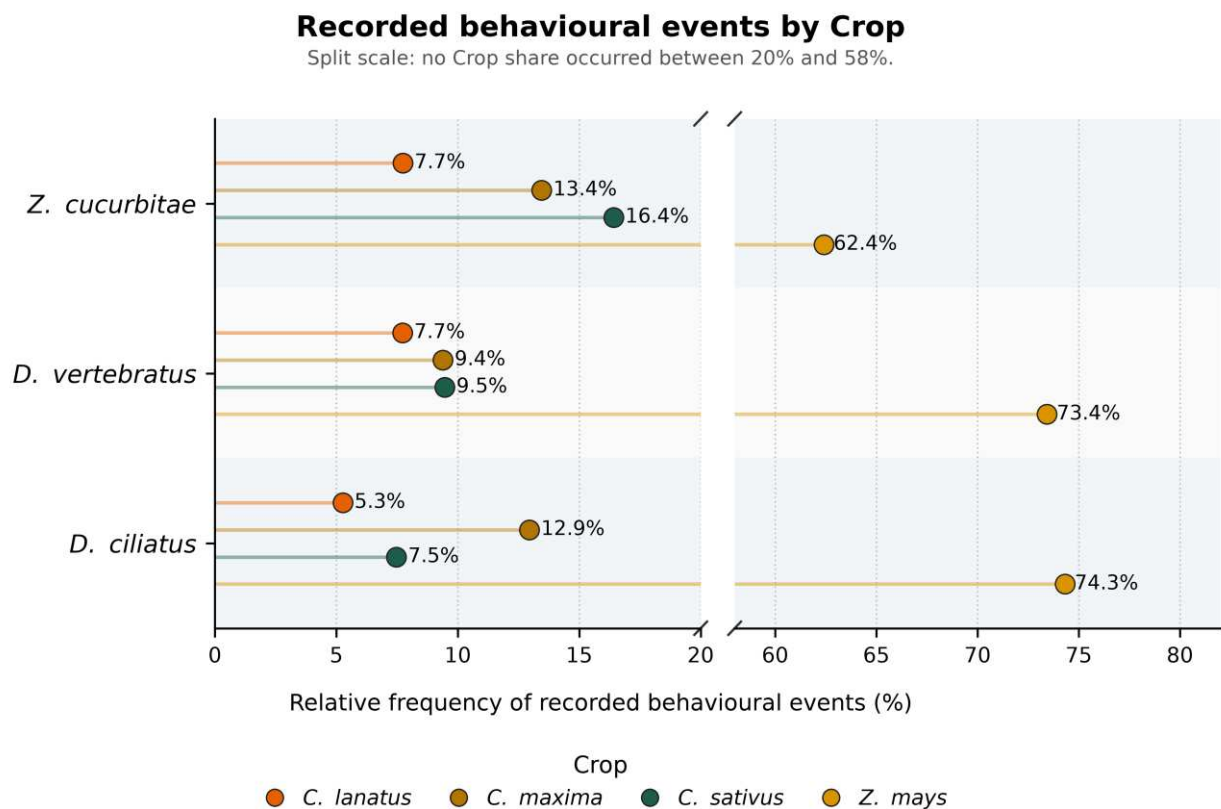


Figure 3. Relative frequency of recorded behavioural events by crop within each fruit-fly species.

Behavioural composition varied over the five observed daytime periods (Fig. 4). Roosting remained the dominant recorded behaviour, declining across successive periods from 90.8% of recorded events in the early morning to 90.0%, 89.0% and 86.0% in the late morning, midday and afternoon, and 85.2% in the evening. Oviposition was 4.6% in the early morning and 4.1% in the late morning, then reached 7.0% at midday, 8.0% in the afternoon and 8.6% in the evening, whereas feeding ranged from 3.2% to 5.9% with no directional pattern across periods. No mating events were recorded from early morning through midday; five were recorded in the afternoon (0.5% of events in that period) and 16 in the evening (3.0%).

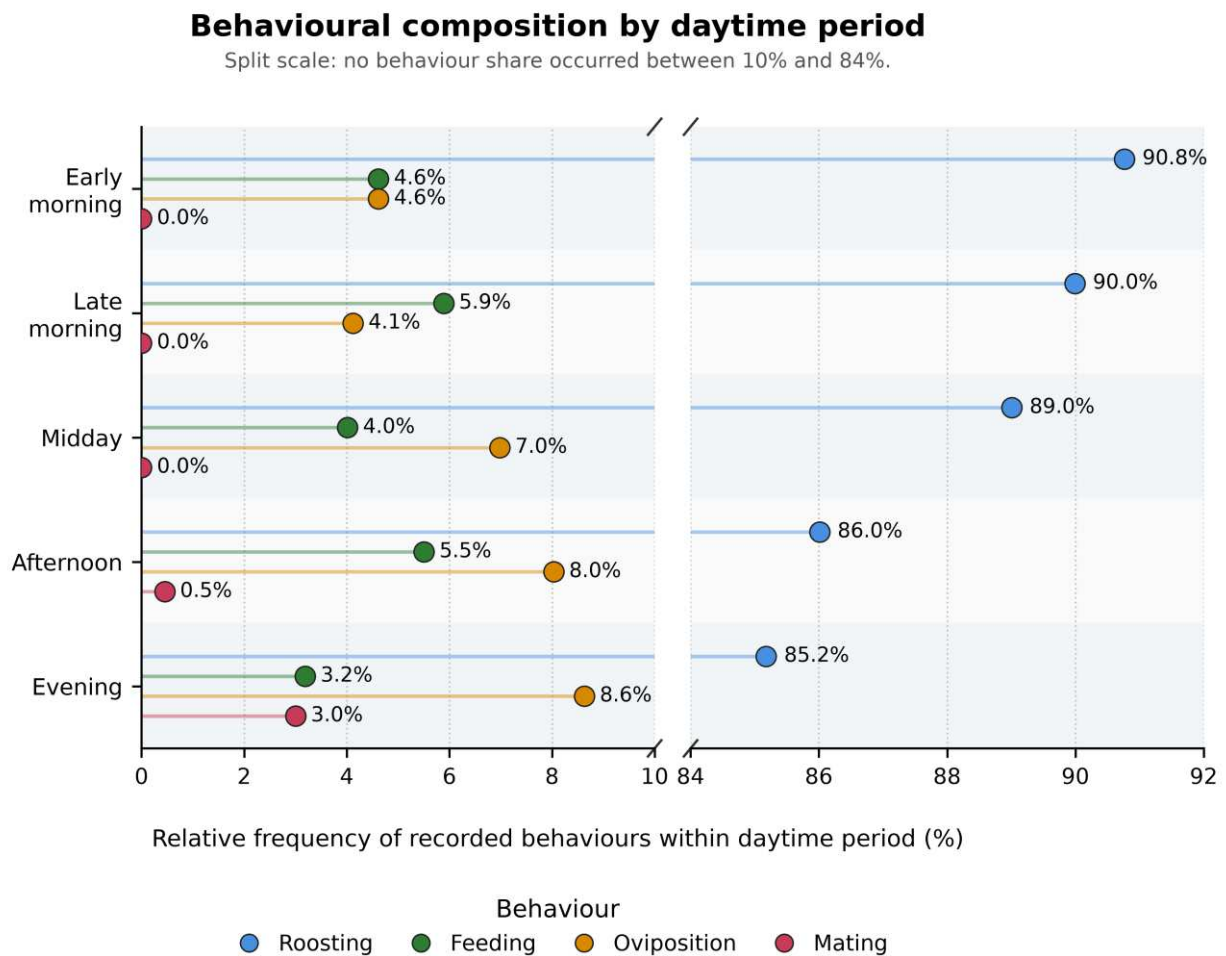


Figure 4. Relative frequency of recorded behavioural events within each daytime period.

Across the study, 4,460 roosting, 313 oviposition, 243 feeding, and 21 mating events were recorded. Behavioural composition was broadly similar among species (Fig. 5): roosting represented 87.7–89.2% of recorded events, oviposition 4.6–6.6%, feeding 4.2–5.9%, and mating 0.3–0.5%. Observed mean counts for each species, crop position and daytime period are given in Supplementary Fig. S1.

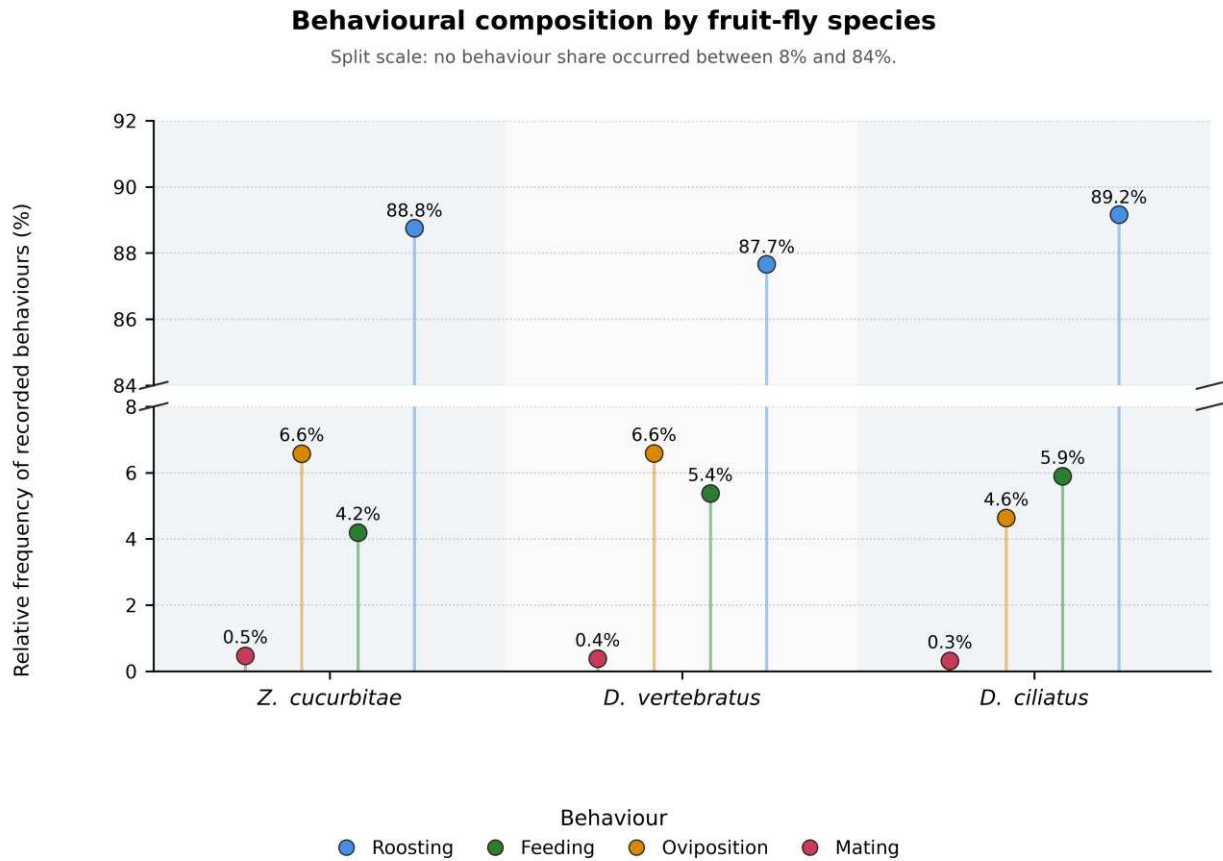


Figure 5. Relative frequency of recorded behavioural events within each fruit-fly species.

Species-specific diel behavioural patterns

Zeugodacus cucurbitae

Zeugodacus cucurbitae showed crop and daytime-period associations for roosting (both $q < .001$; Fig. 6). Observed roosting was greatest on maize, and the fitted daytime peak was 11:09 (95% CI: 09:45–12:05). Feeding was also most frequently observed on maize and varied by crop ($q = .005$), but not by daytime period after FDR adjustment ($q = .168$); its fitted peak was 11:02 (95% CI: 07:49–13:04). Oviposition varied among the three cucurbit host crops and across daytime periods (both $q < .001$), with a fitted peak at 12:53 (95% CI: 11:12–14:13). Thirteen mating events were recorded and are presented descriptively.

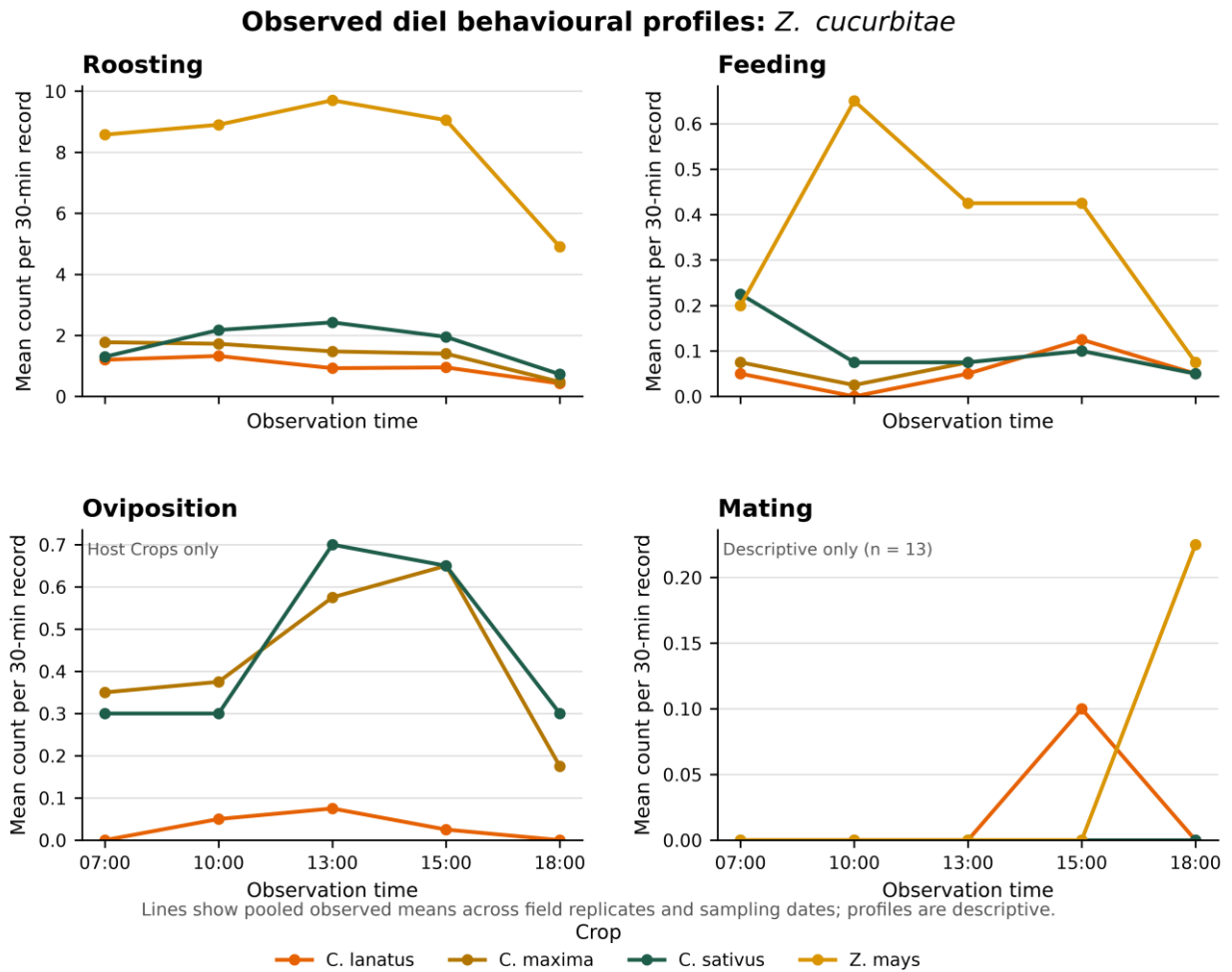


Figure 6. Observed mean behavioural counts per 30-min record by crop and daytime period for *Z. cucurbitae*. Lines pool field replicates and sampling dates. Oviposition is shown for host crops only; mating is descriptive ($n = 13$).

Dacus vertebratus

For *D. vertebratus*, the distribution of roosting among crops changed over the day (crop $\times$ daytime-period interaction: $\chi^2(12) = 50.45$, $q < .001$; Fig. 7). Observed roosting was highest on maize throughout the sampled periods; the fitted peak was 07:59 (95% CI: 07:12–11:38). Feeding varied by crop ($q < .001$), with no FDR-supported daytime-period association ($q = .307$); its fitted peak was 09:34 (95% CI: 07:25–13:21). Oviposition was sparse and had no FDR-supported crop or daytime-period association. Five mating events were recorded and are shown descriptively.

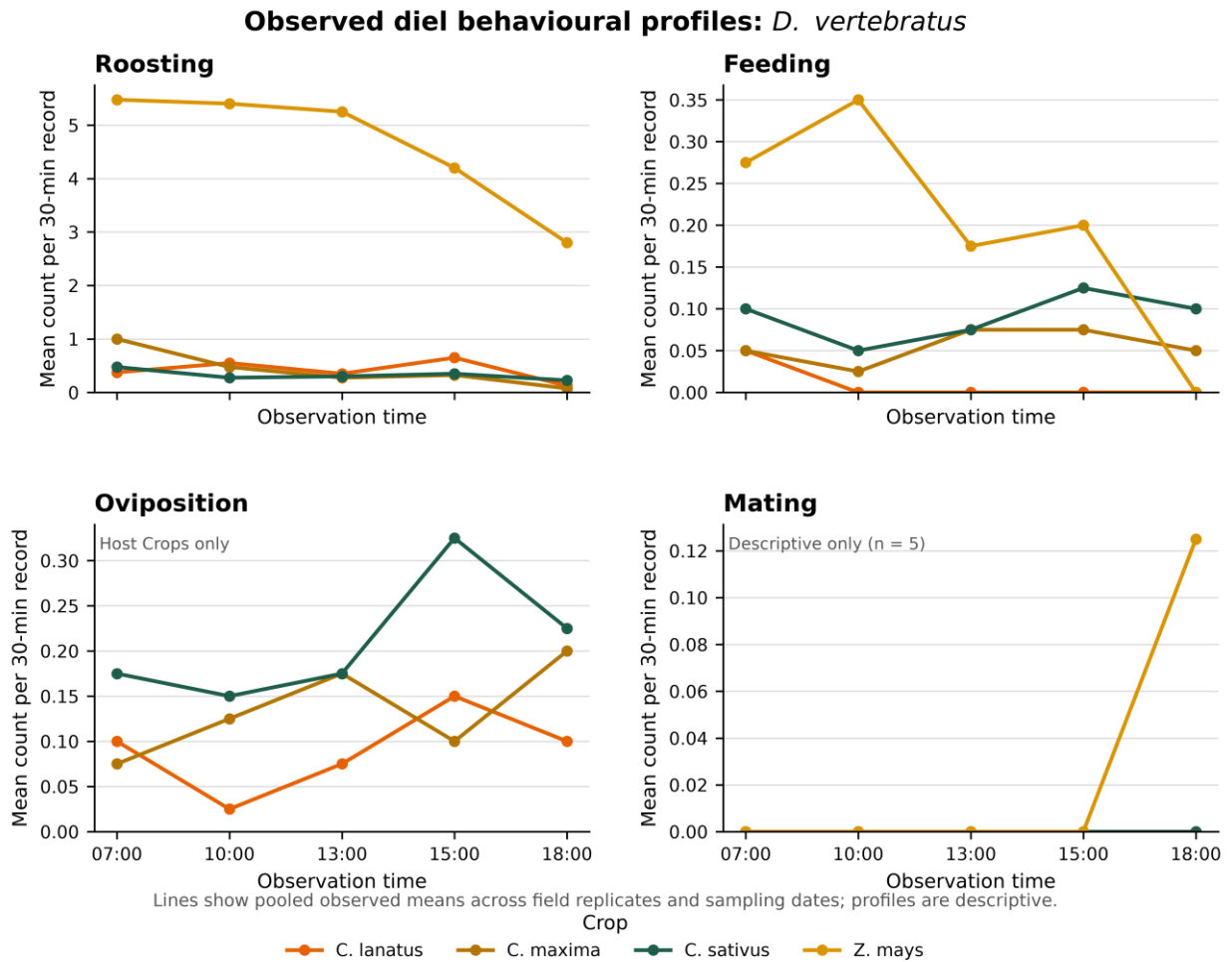


Figure 7. Observed mean behavioural counts per 30-min record by crop and daytime period for *D. vertebratus*. Lines pool field replicates and sampling dates. Oviposition is shown for host crops only; mating is descriptive ($n = 5$).

Dacus ciliatus

In *D. ciliatus*, the crop distribution of roosting also changed through the day (crop $\times$ daytime-period interaction: $\chi^2(12) = 24.10$, $q = .039$; Fig. 8). The fitted roosting peak was 11:31 (95% CI: 09:31–12:38). Feeding was sparse but varied by crop ($q < .001$) and daytime period ($q = .005$), with a fitted peak at 09:19 (95% CI: 07:17–11:36). Oviposition was also sparse, with no FDR-supported crop or daytime-period association; its fitted peak was imprecise at 10:21 (95% CI: 07:45–16:19). Three mating events were recorded and are shown descriptively.

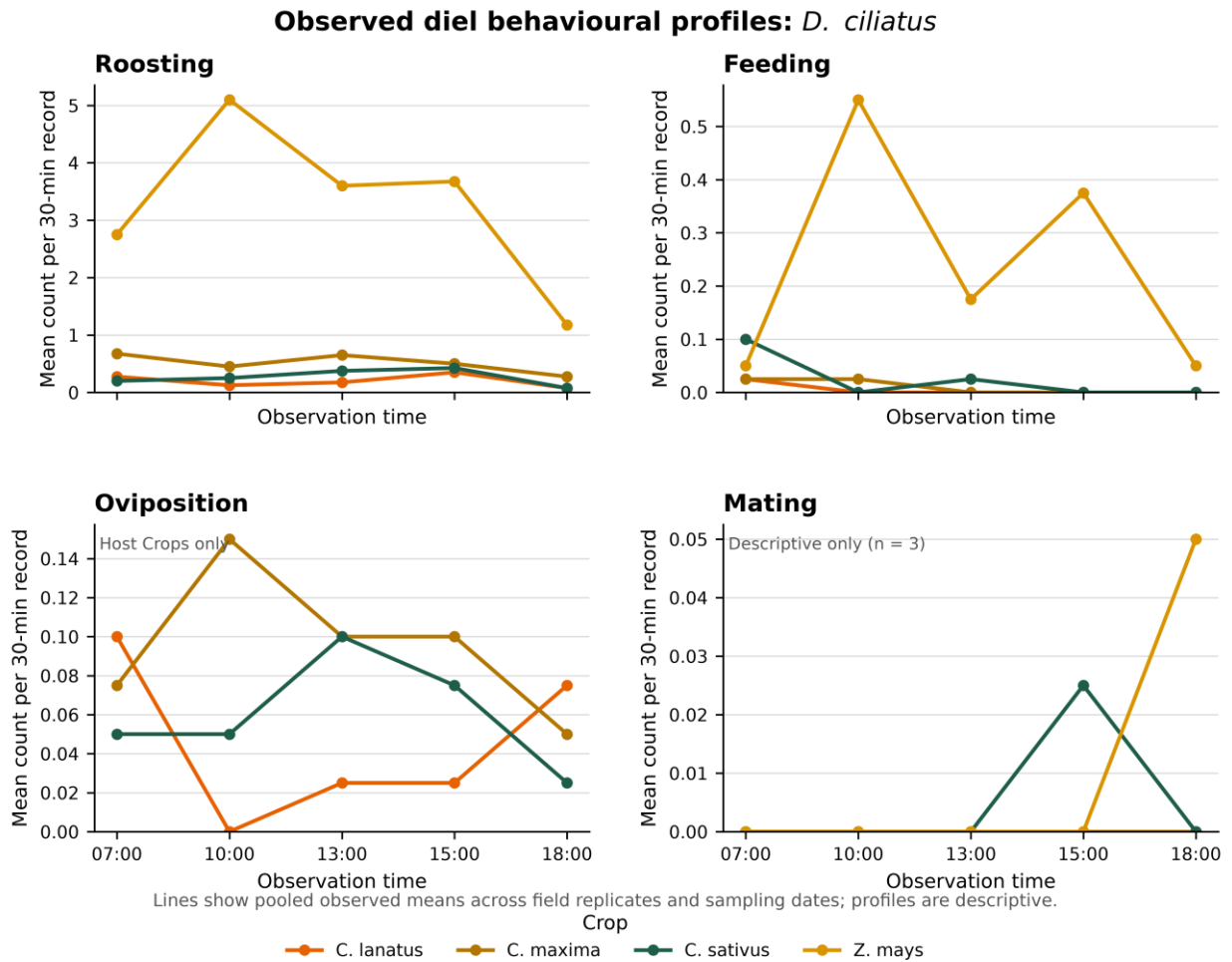


Figure 8. Observed mean behavioural counts per 30-min record by crop and daytime period for *D. ciliatus*. Lines pool field replicates and sampling dates. Oviposition is shown for host crops only; mating is descriptive ($n = 3$).

Interspecific differences in crop use and diel behaviour

Having characterized the diel and crop-use patterns of each species separately, we next examined whether these patterns differed among species and across crops and daytime periods. The supported interactions differed among behaviours (Fig. 9). Roosting showed significant species $\times$ crop and crop $\times$ daytime-period interactions, feeding showed a significant species $\times$ crop $\times$ daytime-period interaction, and oviposition showed a significant species $\times$ crop interaction. The remaining tested interactions were not significant. Mating was not analysed factorially because observations were too few. Pairwise Pianka overlap indices summarizing similarity among species in proportional crop-position and daytime-period use are given in Supplementary Fig. S2. Where a factor was involved in a significant interaction, interpretation focused on the interaction rather than its corresponding main effect.

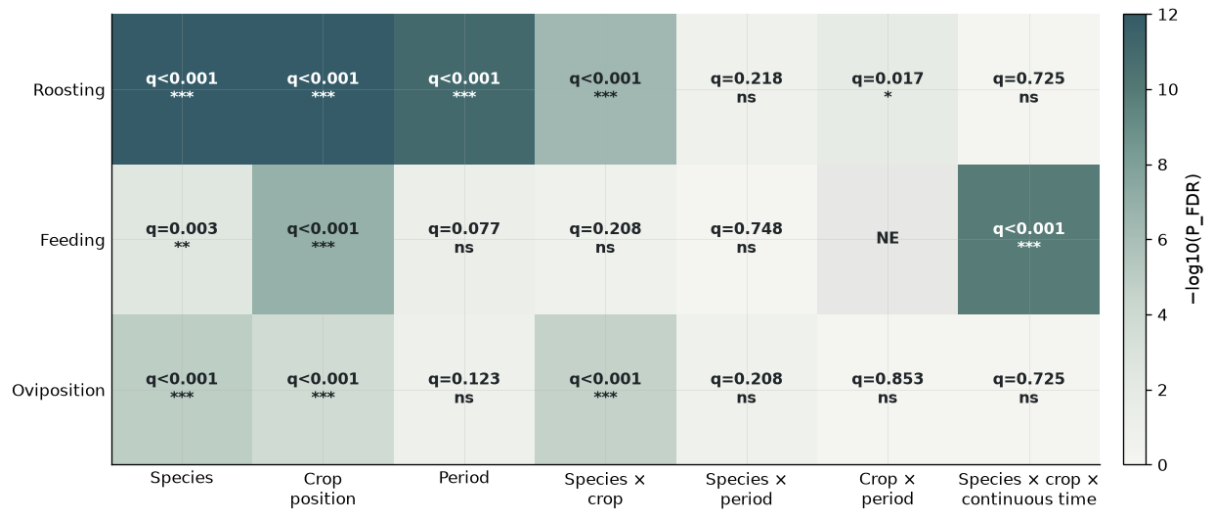


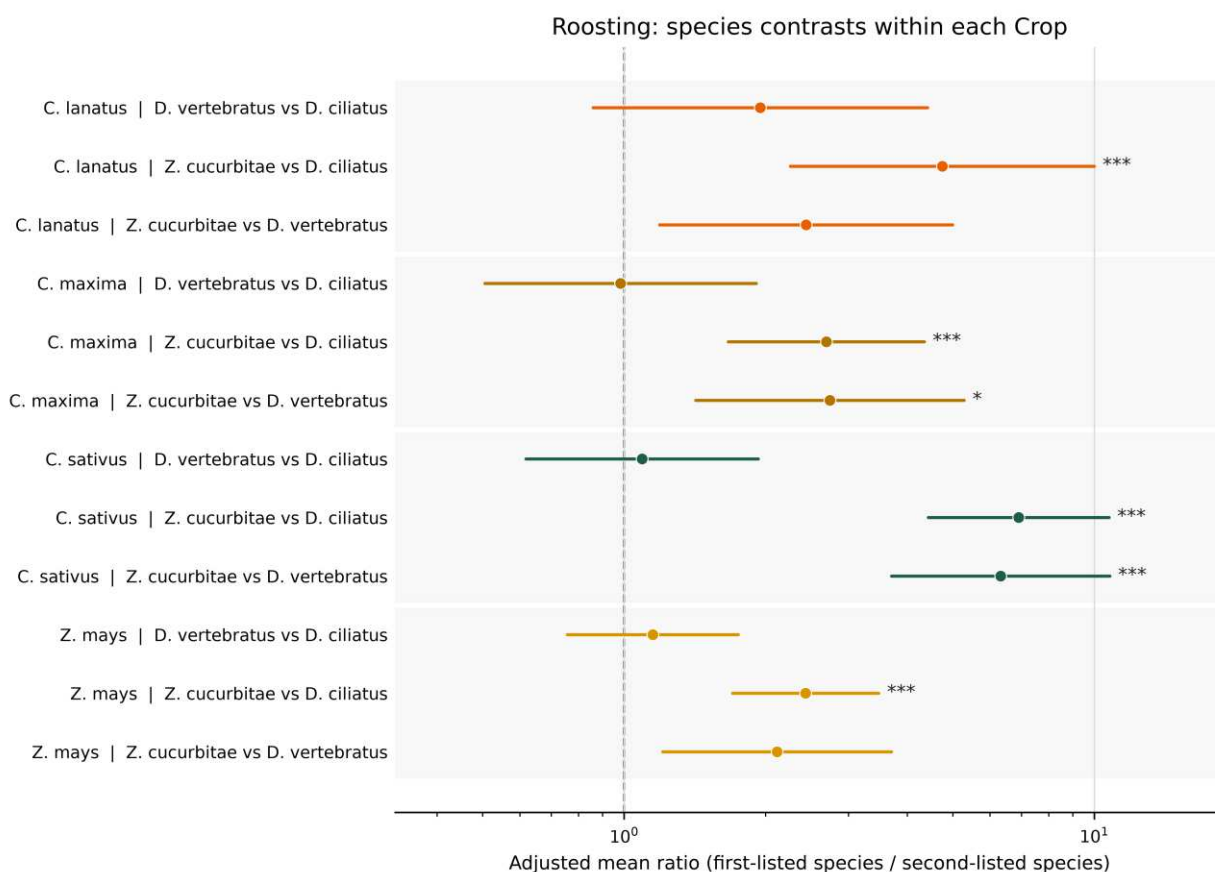
Figure 9. FDR-screened pooled associations and interactions. Cells summarize joint Wald tests from the pooled negative-binomial GEE models for species, crops, daytime period, and prespecified interactions. Displayed values are Benjamini–Hochberg FDR-adjusted p values; darker cells indicate stronger evidence. Oviposition excludes the maize border from its target population, and mating was not modelled factorially.

Effects of species, crop and daytime period on behaviour

Follow-up contrasts for supported interactions are presented in Figs. 10–12, while the exploratory reduced feeding model is presented in Fig. 11. Pairwise inference used Holm-adjusted P values; horizontal intervals are pointwise 95% confidence intervals.

Roosting

Adjusted roosting counts for *Z. cucurbitae* were significantly higher than those for *D. ciliatus* on all four crops: 4.75-fold on *C. lanatus* (95% CI: 2.26–10.00; Holm $P < .001$), 2.69-fold on *C. maxima* (1.67–4.35; $P < .001$), 6.91-fold on *C. sativus* (4.44–10.75; $P < .001$), and 2.43-fold on maize (1.70–3.48; $P < .001$; Fig. 10). Compared with *D. vertebratus*, *Z. cucurbitae* also had higher adjusted roosting counts on *C. maxima* (2.74-fold, 1.42–5.29; Holm $P = .019$) and *C. sativus* (6.32-fold, 3.70–10.79; $P < .001$). No other pairwise differences were significant after Holm adjustment.



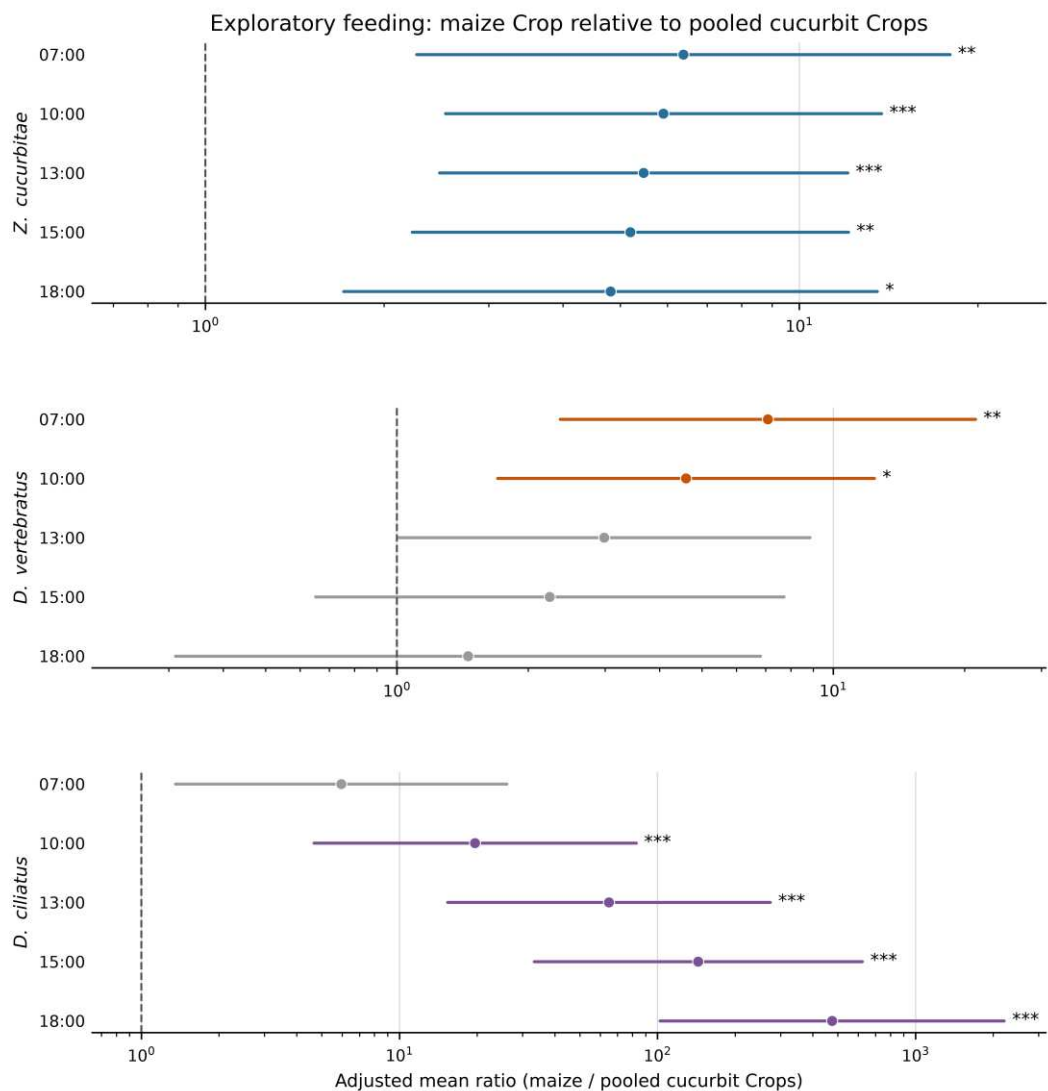
Whiskers = pointwise 95% confidence intervals. Asterisks denote Holm-adjusted $P < .05$.

Figure 10. Pairwise fold changes in model-adjusted mean roosting counts between species within each crop. Points and whiskers show estimates and pointwise 95% confidence intervals; P values were Holm-adjusted across the 12 comparisons. Ratios above 1 favour the first-listed species.

Feeding

The exploratory reduced model showed that differences in feeding between maize and the pooled cucurbit crops varied over the day among species (Fig. 11). For *Z. cucurbitae*, adjusted feeding counts were higher on maize at all five representative daytime-period midpoints, with ratios of 4.81–6.38 and Holm-adjusted $P \leq .016$. For *D. vertebratus*, the contrast was supported in the early morning (7.08-fold, 95% CI: 2.37–21.17; Holm $P = .004$) and late morning (4.60-fold, 1.70–12.43; $P = .016$), but not later in the day. For *D. ciliatus*, the contrast was supported from late morning through evening, although estimates were imprecise because feeding was sparse; the early-morning contrast did not survive Holm adjustment ($P = .073$). In a two-abundant-species sensitivity analysis excluding *D. ciliatus*, the reduced interaction was not supported [$\chi^2(1) = 2.88$, $P = .090$]. These exploratory results compare maize with the three

318 cucurbit crops pooled together and therefore do not represent feeding patterns on individual
 319 cucurbit crops.



320 Whiskers = pointwise 95% confidence intervals; asterisks denote Holm-adjusted $P < .05$. Panel-specific log scales are used because of sparse *D. ciliatus* feeding.

321 **Figure 11. Exploratory fold changes in model-adjusted feeding counts for maize crop**
 322 **relative to pooled cucurbit crops at the five daytime-period midpoints. Points and**
 323 **whiskers show estimates and pointwise 95% confidence intervals; P values were Holm-**
 324 **adjusted across 15 contrasts. This reduced continuous-time model is not a full individual-**
 325 **crop $\times$ categorical daytime-period analysis. Panel-specific log scales are used because *D.***
 326 ***ciliatus* feeding was sparse.**

327 Oviposition

328 *Z. cucurbitae* had higher adjusted oviposition counts than *D. vertebratus* on *C. maxima* (3.41-
 329 fold, 95% CI: 1.61–7.21; Holm $P = .009$), and higher counts than *D. ciliatus* on *C. maxima*

(4.17-fold, 1.99–8.72; $P = .001$) and *C. sativus* (8.87-fold, 4.07–19.37; $P < .001$; Fig. 12). The remaining interspecific comparisons did not survive Holm adjustment.

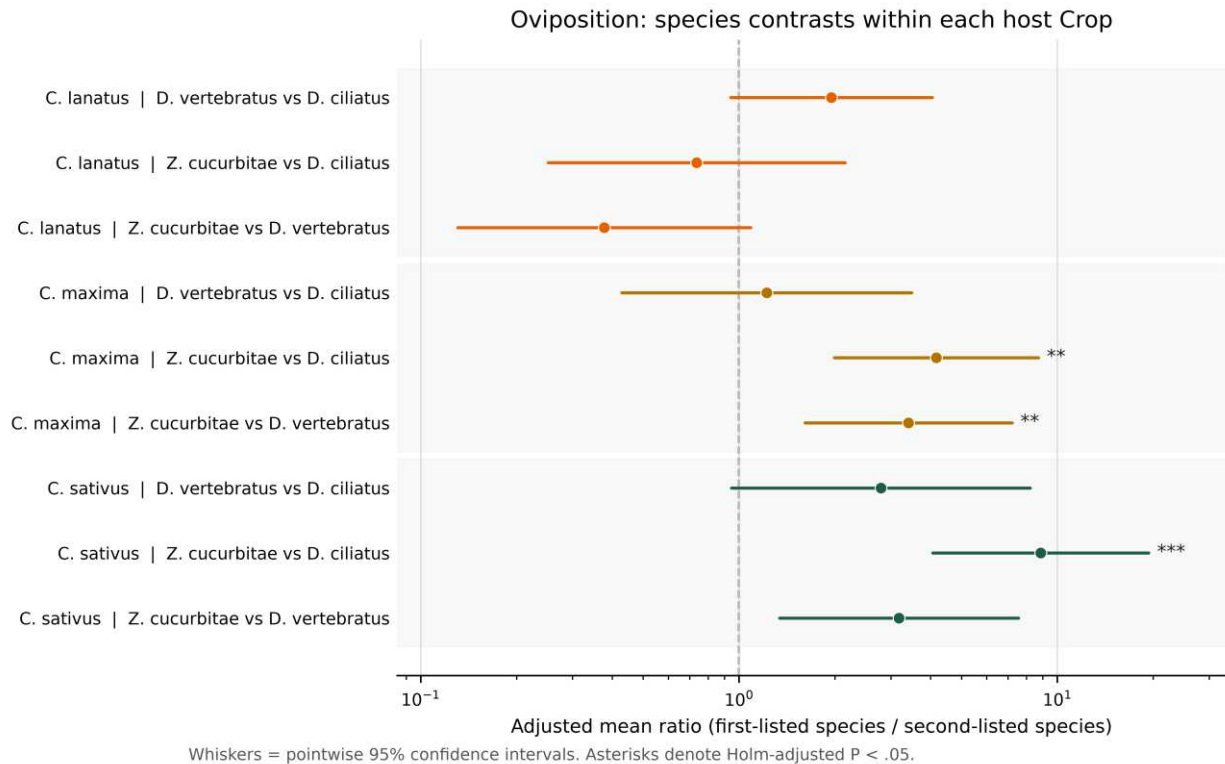


Figure 12. Pairwise fold changes in model-adjusted mean oviposition counts between species within each host crop. Points and whiskers show estimates and pointwise 95% confidence intervals; P values were Holm-adjusted across the nine comparisons. Maize was excluded because it was not an oviposition host. Ratios above 1 favour the first-listed species.

Marginal residual diagnostic screens indicated departures for the *D. vertebratus* and *D. ciliatus* roosting models (Kolmogorov–Smirnov $P < .001$ and $P = .005$, respectively) and their oviposition models ($P = .004$ and $P = .045$). Because these screens did not reproduce the GEE working correlation, they are treated as diagnostic cautions rather than formal lack-of-fit tests.

Site and weather associations

Site-related differences were limited and depended on species and daytime period (Fig. 13). Roosting by *D. vertebratus* and *D. ciliatus* was higher at Crop Museum, while site differences were also observed for early-morning feeding and evening oviposition. However, these contrasts cannot be attributed specifically to site, elevation or agroecological zone because

these factors, together with other local conditions, were not independently separated by the two-site design.

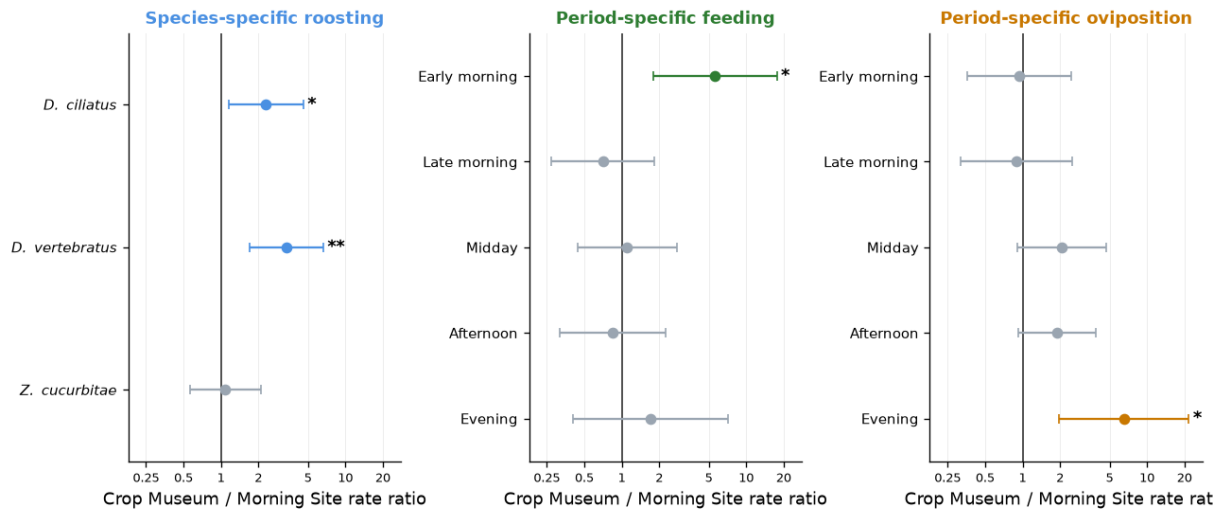


Figure 13. Site-related differences in behavioural activity. Points show adjusted-count ratios for Crop Museum relative to Morning Site with 95% confidence intervals. Ratios above 1 indicate higher activity at Crop Museum.

Weather conditions varied strongly between sites and across daytime periods (Fig. 14). When examined individually, shortwave radiation was positively associated with roosting and temperature was associated with some behaviours. However, after accounting for daytime period, none of the measured weather variables remained FDR-supported, indicating no clear additional behavioural association beyond the diel pattern.

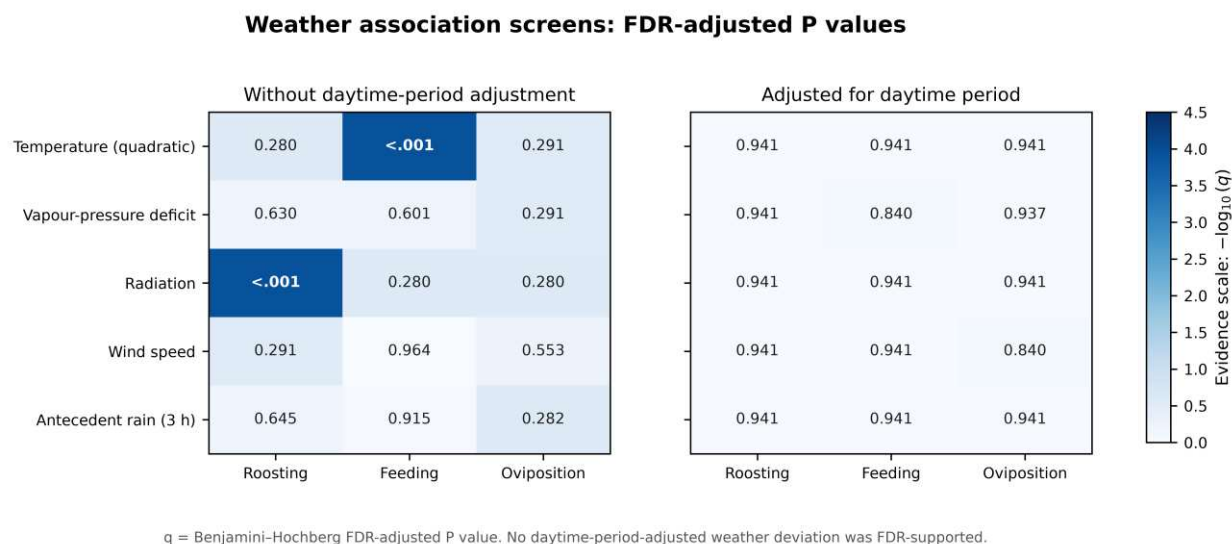


Figure 14. FDR-adjusted P values from weather–activity association screens. The left panel shows weather-exposure models without daytime-period adjustment; the right panel retains daytime period and tests the corresponding within-period weather deviation. Relative humidity was not fitted as a predictor. No right-panel test was FDR-supported.

Discussion

We recorded diel behavioural patterns of roosting, feeding, oviposition and mating by *Z. cucurbitae*, *D. vertebratus* and *D. ciliatus*. The three species differed not only in their use of crops but also in how some behaviours varied across the day, indicating that crop use and diel activity were behaviour- and species-dependent. Oviposition showed species-specific host use, with *Z. cucurbitae* showing the strongest differentiation among cucurbit hosts. Some of the most important factors influencing fruit fly oviposition behaviour include host quality (i.e., size, colour, penetrability and degree of ripeness), presence of host-marking pheromone and competition⁶⁵. Surface characteristics may also influence insect choice for feeding and oviposition⁶⁶. Oviposition preferences of *Z. cucurbitae* for cucumber and pumpkin have been reported previously^{67,68}, while host-dependent differences have also been reported among cucurbit hosts⁶⁹. A distinct diel pattern of oviposition was most evident in *Z. cucurbitae*, with activity concentrated around midday. Similarly, oviposition by *Anastrepha fraterculus* occurred throughout the day and extended into dusk⁷⁰, while *Z. cucurbitae* and *Z. tau* show different diel oviposition patterns under laboratory conditions⁷¹. Such variation is consistent with species-specific differences in the timing and host use of tephritid oviposition⁷². Thus, in

our study, interspecific differentiation in oviposition was expressed mainly through host use, while the clearest diel pattern occurred in *Z. cucurbitae*.

Roosting was the dominant behaviour recorded for all three species, with maize serving as the principal roosting site. However, roosting patterns were not uniform: crop use differed among species and also varied across daytime periods, as indicated by the significant species $\times$ crop and crop $\times$ daytime-period interactions. The latter suggests that the use of particular crops for roosting changed over the course of the day rather than remaining constant. The strong use of maize is consistent with the importance of non-host vegetation as resting or refuge sites for fruit flies within cropping systems. Such vegetation may therefore serve not simply as a static refuge, but as a component of the crop environment whose use changes with diel activity.

Feeding showed a more complex pattern. The categorical three-way feeding model was non-estimable, but the reduced exploratory model indicated that the maize-to-cucurbit contrast changed over the day differently among species. Thus, feeding differences among the three species involved not simply the amount of feeding activity, but species-specific combinations of crop use and diel timing. The high feeding activity on maize does not necessarily indicate feeding on maize itself, but may reflect nutritional resources available on its surfaces. Feeding patterns can also vary among tephritids; female *Ceratitis cosyra*, *C. fasciventris* and *C. capitata* may feed relatively uniformly throughout the day, whereas males of some species show morning or afternoon peaks⁷³.

Taken together, the three behaviours revealed different forms of interspecific differentiation. Roosting differed in both species-specific crop use and diel use of crops; oviposition showed clear species-specific host use; and feeding, on exploratory evidence, depended jointly on species, crop and daytime period. Rather than following a single common pattern of crop use across the day, the species differed in how particular behaviours were distributed in space and time. This comparative information is particularly valuable for *D. vertebratus* and *D. ciliatus*, for which detailed diel behavioural information remains limited compared with *Z. cucurbitae*.

Site-related differences were limited but occurred for particular species and daytime periods, including higher roosting by *D. vertebratus* and *D. ciliatus* at Crop Museum and differences in early-morning feeding and evening oviposition. These differences may reflect variation in local environmental conditions between the two sites. However, because site, elevation,

agroecological zone and other local conditions varied together, their individual contributions cannot be separated in the present study.

Although diel activity in fruit flies may occur within a broader circadian framework, our observations under natural field conditions describe diel patterns rather than demonstrating endogenous circadian rhythms. Experimental studies have shown that feeding, locomotion, mating and oviposition in fruit flies can be influenced by endogenous clocks, light-dark transitions and social conditions. Weather conditions varied between sites and across daytime periods, and some behaviours were associated with shortwave radiation and temperature when these variables were considered individually. However, these associations weakened after daytime period was accounted for, and none of the measured weather variables provided clear additional explanatory power beyond the underlying diel pattern. Thus, the observed diel patterns cannot be attributed independently to any single measured weather variable, although temperature, radiation, humidity and other environmental conditions may contribute to behavioural variation across the day.

This study has determined the diel behavioural patterns of roosting, feeding, mating and oviposition of cucurbit-infesting fruit flies in relation to crop use and time of day. This information may help improve the timing and targeting of fruit fly control as part of more effective and sustainable management strategies. In particular, the strong use of maize for roosting and its involvement in species- and time-dependent feeding patterns suggests that non-host vegetation may provide a useful spatial target for interventions such as spot application of protein or toxic baits^{1,2,23,74}. However, because maize occupied a fixed border position in this study, this potential management application should be experimentally tested before broader recommendation.

Temporal targeting may also improve intervention efficiency where behaviours show clear diel concentrations. The midday concentration of *Z. cucurbitae* oviposition, for example, identifies a period when females may be more likely to occur on host crops, while the strong use of non-host vegetation for roosting provides a complementary spatial target. The species-specific crop and diel patterns observed for feeding further suggest that the effectiveness of spatial targeting may depend on when interventions are applied. Mating-based control may similarly benefit from knowledge of reproductive timing, but the small number of mating observations in this study does not justify a precise operational recommendation. More generally, combining information on where flies perform particular behaviours with when those behaviours are most

frequently observed may provide a stronger basis for behavioural management than relying on abundance alone.

Further research is necessary to experimentally test the role of non-host vegetation, host quality and microhabitat in shaping these diel behavioural patterns and to extend observations into dusk and night, particularly for mating. Studies that independently separate site, elevation, agroecological zone and local environmental conditions would also help determine the factors underlying the site-related differences observed here. Continuous observations under controlled light-dark conditions would be required to distinguish field diel patterns from endogenous circadian regulation. Such studies are particularly needed for *D. vertebratus* and *D. ciliatus*, for which detailed temporal behavioural information remains limited.

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Author contributions

PMB, ABK, MWM, MDM, JPD, MV, and RM conceived and designed the study. JB, SAK, JCT, and EWR collected data and drafted. JOR performed data analysis and visualizations. All authors reviewed and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Availability of data and materials

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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475 **References**

- 476 1. Deguine, J. P., Atiama-Nurbel, T., Douraguia, E., Chiroleu, F. & Quilici, S. Species diversity
477 within a community of the cucurbit fruit flies *Bactrocera cucurbitae*, *Dacus ciliatus*,
478 and *Dacus demmerezi* roosting in corn borders near cucurbit production areas of
479 Reunion Island. *Journal of Insect Science*, 12(1) (2012).
- 480 2. Deguine, J.-P., Rousse, P. & Atiama-Nurbel, T. Agroecological crop protection: concepts
481 and a case study from Reunion. In *Integrated Pest Management and Pest Control:*
482 *Current and Future Tactics* (pp. 63–76). Intech Publisher (2012).
- 483 3. Ormsby, M. D. Establishing criteria for the management of tephritid fruit fly outbreaks.
484 *CABI Agriculture and Bioscience* 2, 1–22 (2021).
- 485 4. Nair, N., Chatterjee, M., Das, K., Sehgal, M. & Malik, M. Fruit Fly Species Complex
486 Infesting Cucurbits in India and Their Management. *International Journal of*
487 *Agriculture, Environment and Sustainability* 3, 8–17 (2021).
- 488 5. Ganie, S. A. et al. Fruit Fly Management and Control Strategies: A Review. *Biopesticides*
489 *International* 18, 89–100 (2022).
- 490 6. Sapkota, R., Dahal, K. C. & Thapa, R. B. Damage assessment and management of cucurbit
491 fruit flies in spring-summer squash. *Journal of Entomology and Nematology* 2, 7–12
492 (2010).
- 493 7. Pinero, J. C., Souder, S. K., Cha, D. H., Collignon, R. M. & Vargas, R. I. Age-dependent
494 response of female melon fly, *Zeugodacus cucurbitae* (Diptera: Tephritidae), to
495 volatiles emitted from damaged host fruits. *Journal of Asia-Pacific Entomology* 24,
496 759–763 (2021).
- 497 8. Kubar, M. I., Khoso, F. N., Khatri, I., Khuhro, N. H. & Gilal, A. A. Effect of Different
498 Management Strategies on Melon Fruit Fly, *Bactrocera cucurbitae* (Coquillett),
499 Infestation in Cucurbit Vegetables. *Sarhad Journal of Agriculture* 37, 915–920 (2021).
- 500 9. Sahu, B. K. & Samal, I. Pest complex of Cucurbits and their management: A review. *Journal*
501 *of Entomology and Zoology Studies* 8, 89–96 (2020).
- 502 10. Sarkar, R., Das, S., Kamal, M. M., Islam, K. S. & Jahan, M. Efficacy of management
503 approaches against cucurbit fruit fly (*Bactrocera cucurbitae* coquillett) of bitter gourd.
504 *Bangladesh Journal of Agricultural Research* 42, 757–766 (2017).

- 505 11. Sohrab, W. H. & Prasad, C. S. Investigation on Level of Infestation and Management of
506 Cucurbit Fruit Fly, *Bactrocera cucurbitae* (Coquillett) in Different Cucurbit Crops.
507 International Journal of Pure & Applied Bioscience 6, 184–196 (2018).
- 508 12. Vänninen, I. Alternatives to pesticides in fruit and vegetable cultivation. In W. Jongen
509 (Ed.), Woodhead Publishing Series in Food Science, Technology and Nutrition (pp.
510 293–330). Woodhead Publishing (2005).
- 511 13. Amala, U. & Shivalingaswamy, T. M. Effect of intercrops and border crops on the diversity
512 of parasitoids and predators in agroecosystem. Egyptian Journal of Biological Pest
513 Control 28, 11 (2018).
- 514 14. Deguine, J. P. et al. Agroecological management of cucurbit-infesting fruit fly: a review.
515 Agronomy for Sustainable Development 35, 937–965 (2015).
- 516 15. Lamont, E. W. & Amir, S. Circadian and Ultradian Clocks/Rhythms. In G. F. Koob, M. Le
517 Moal, & R. F. Thompson (Eds.), Encyclopedia of Behavioral Neuroscience (pp. 257–
518 261). Academic Press (2010).
- 519 16. Refinetti, R. Biological Rhythms. In S. E. Jørgensen & B. D. Fath (Eds.), Encyclopedia of
520 Ecology (pp. 420–426). Academic Press (2008).
- 521 17. Meireles-Filho, A. C. A. & Kyriacou, C. P. Circadian rhythms in insect disease vectors.
522 Memórias Do Instituto Oswaldo Cruz, 108((suppl 1)), 48–58. <https://doi.org/> (2013).
- 523 18. Numata, H., Miyazaki, Y. & Ikeno, T. Common features in diverse insect clocks.
524 Zoological Letter, 1(10) (2015).
- 525 19. Helfrich-Förster, C. Light input pathways to the circadian clock of insects with an emphasis
526 on the fruit fly *Drosophila melanogaster*. Journal of Comparative Physiology A 206,
527 259–272 (2020).
- 528 20. Bertolini, E. et al. The characterization of the circadian clock in the olive fly *Bactrocera*
529 *oleae* (Diptera: Tephritidae) reveals a *Drosophila*-like organization. Scientific Reports
530 8, 816 (2018).
- 531 21. Shelly, T. & Kurashima, R. Field capture of male Mediterranean fruit flies (Diptera:
532 Tephritidae) in traps baited with varying amounts of trimedlure. Florida Entomologist
533 103, 16–22 (2020).
- 534 22. Díaz-Fleischer, F., Pérez-Staples, D., Cabrera-Mireles, H., Montoya, P. & Liedo, P. Novel
535 insecticides and bait stations for the control of *Anastrepha* fruit flies in mango orchards.
536 Journal of Pest Science 90, 865–872 (2017).

23. Atiama-Nurbel, T., Deguine, J. P. & Quilici, S. Maize more attractive than Napier grass as non-host plants for *Bactrocera cucurbitae* and *Dacus demmerezi*. *Arthropod-Plant Interactions* 6, 395–403 (2012).
24. Layodé, B. F. R., Onzo, A. & Karlsson, M. F. Watermelon-infesting Tephritidae fruit fly guild and parasitism by *Psytalia phaeostigma* (Hymenoptera: Braconidae). *International Journal of Tropical Insect Science* 40, 157–166 (2020).
25. Nage, S., Kulkarni, U. S., Undirwade, D. B., Meshram, N. M. & Sant, S. The species composition, richness and diversity studies of fruit flies captured from the orchard of Nagpur mandarin. *Scientific Reports* 13, 21872 (2023).
26. Isabirye, B. E., Akol, A. M., Mayamba, A., Nankinga, C. K. & Rwomushana, I. Species composition and community structure of fruit flies (Diptera: Tephritidae) across major mango-growing regions in Uganda. *International Journal of Tropical Insect Science* 35, 69–79 (2015).
27. Jedyi, H., Naamani, K., Ait Elkoch, A. & El Keroumi, A. First Study of Diptera Seasonal Dynamics and their Community Structure in Moroccan Vineyards. *African Entomology* 28, 312–328 (2020).
28. Mwatawala, M. et al. Preference of *Zeugodacus cucurbitae* (Coquillett) for three commercial fruit vegetable hosts in natural and semi natural conditions. *Fruits* 70, 333–339 (2015).
29. Nanga Nanga, S. et al. Tephritid Fruit Fly Species Composition, Seasonality, and Fruit Infestations in Two Central African Agro-Ecological Zones. *Insects* 13, 1045 (2022).
30. Vayssières, J. F., Korie, S., Coulibaly, O., Temple, L. & Boueyi, S. The mango fruit fly, *Bactrocera invadens*, in Benin: Trap efficiency, host range and seasonality. *Fruits* 64, 335–348 (2009).
31. Geurts, K., Mwatawala, M. W. & De Meyer, M. Dominance of an invasive fruit fly species, *Bactrocera invadens*, along an altitudinal transect in Morogoro, Eastern Central Tanzania. *Bulletin of Entomological Research* 104, 288 (2014).
32. Geurts, K., Mwatawala, M. & De Meyer, M. Indigenous and invasive fruit fly diversity along an altitudinal transect in Eastern Central Tanzania. *Journal of Insect Science* 12, 12 (2012).
33. Hassani, I. M., Delatte, H., Ravaomanarivo, L. H. R., Nouhou, S. & Duyck, P. F. Niche partitioning via host plants and altitude among fruit flies following the invasion of *Bactrocera dorsalis*. *Agricultural and Forest Entomology* 24, 575–585 (2022).

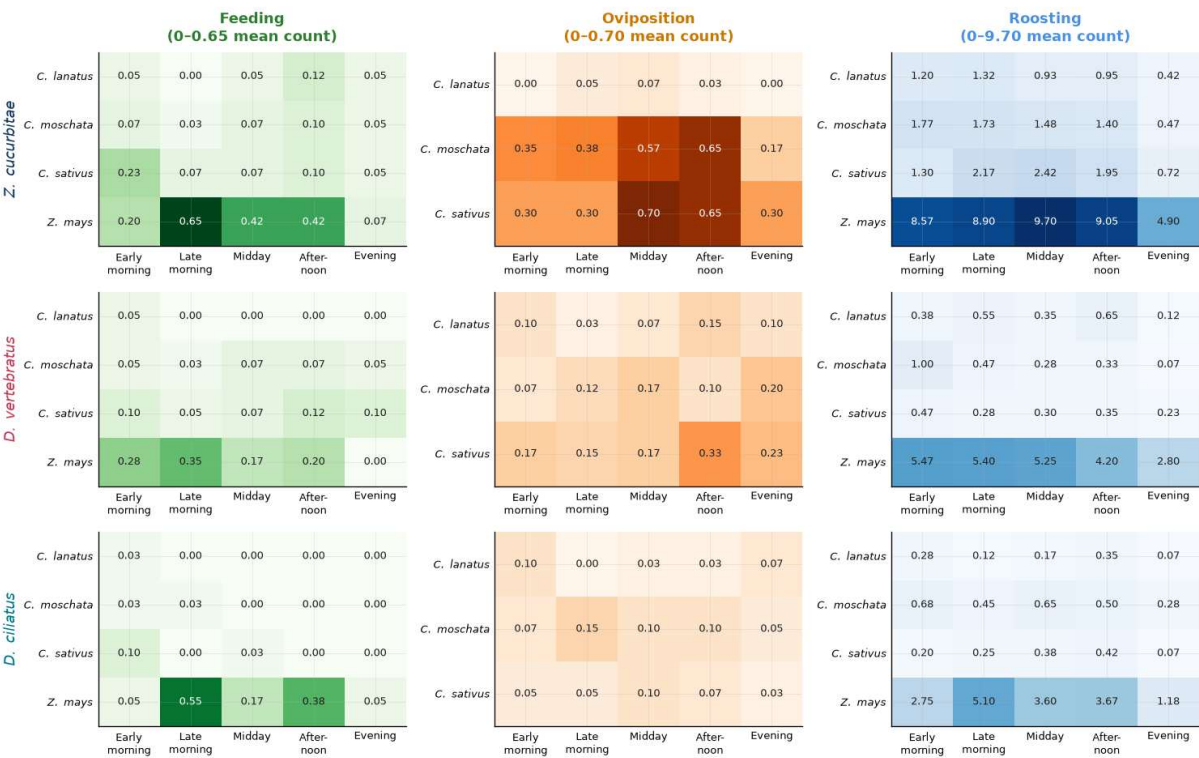
- 570 34. Mwatawala, M., De Meyer, M., Makundi, R. H. & Maerere, A. P. Seasonality and host
571 utilization of the invasive fruit fly, *Bactrocera invadens* (Dipt., Tephritidae) in central
572 Tanzania. *Journal of Applied Entomology* 130, 530–537 (2006).
- 573 35. Duyck, P. F., David, P. & Quilici, S. A review of relationships between interspecific
574 competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology*
575 29, 511–520 (2004).
- 576 36. Mwatawala, M. W. Biodiversity and Bionomics for Fruit Flies (Diptera: Tephritidae) in
577 Morogoro, Tanzania. *Journal of Forestry and Nature Conservation* 79, 43–57 (2009).
- 578 37. Mwatawala, M. W., De Meyer, M., Makundi, R. H. & Maerere, A. P. Host range and
579 distribution of fruit-infesting pestiferous fruit flies (Diptera, Tephritidae) in selected
580 areas of Central Tanzania. *Bulletin of Entomological Research* 99, 629–641 (2009).
- 581 38. Abdulla, N. R., Rwegasira, G. M. & Mwatawala, M. W. Efficacy of African weaver ant,
582 *Oecophylla longinoda* (Hymenoptera: Formicidae) in reducing losses due to
583 frugivorous fruit flies (Diptera: Tephritidae) in smallholder mango production systems
584 in Eastern Tanzania. *Biocontrol Science and Technology* 27, 1205–1219 (2017).
- 585 39. Vayssières, J. F. & Peterson, A. T. Ecological niche modeling of fruit fly species
586 (*Bactrocera*) in Africa and the Middle East. *International Journal of Pest Management*
587 56, 191–201 (2010).
- 588 40. Duyck, P. F., David, P. & Quilici, S. Climatic niche partitioning following successive
589 invasions by fruit flies in La Réunion. *Journal of Animal Ecology* 75, 518–526 (2006).
- 590 41. Bakengesa, J. A. et al. Agroecological farming practices against fruit flies in Central
591 Eastern Tanzania. *FRUITS* 78, 1–12 (2023).
- 592 42. De Blasis, F. Global horticultural value chains, labour and poverty in Tanzania. *World*
593 *Development Perspectives* 18, 100201 (2020).
- 594 43. URT. NATIONAL HORTICULTURE DEVELOPMENT STRATEGY AND ACTION
595 PLAN 2021-2031No Title.
596 [https://doi.org/https://www.kilimo.go.tz/uploads/books/Mkakati_wa_Kuendeleza_Hor](https://doi.org/https://www.kilimo.go.tz/uploads/books/Mkakati_wa_Kuendeleza_Horticulture.pdf)
597 [ticulture.pdf](https://doi.org/https://www.kilimo.go.tz/uploads/books/Mkakati_wa_Kuendeleza_Horticulture.pdf) (2021).
- 598 44. Msafiri, D. & Mwombela, S. Enhancing Competitiveness of Horticultural Industry in
599 Tanzania (2021).
- 600 45. Ekka, R. & Mjawa, B. Case study growth of Tanzania’s horticulture sector: role of TAHA
601 in reducing food loss. USAID (2020).

46. Mwatawala, M. W., Maerere, A. P., Makundi, R. & de Meyer, M. Incidence and host range of the melon fruit fly *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) in Central Tanzania. *International Journal of Pest Management* 56, 265–273 (2010).
47. Fiore, V. et al. The socio-economic issues of agroecology: a scoping review. *Agricultural and Food Economics* 12, 40 (2024).
48. Kerr, A. W. B. G. H. R. B. Agroecological principles and elements and their implications for transitioning to sustainable food systems. A review. *Agronomy for Sustainable Development* 40, 13 (2018).
49. Wezel, A. et al. Agroecological practices for sustainable agriculture. A review. *Agronomy for Sustainable Development* 34, 1–20 (2014).
50. Mziray, H. A., Makundi, R. H., Mwatawala, M., Maerere, A. & De Meyer, M. Host use of *Bactrocera latifrons*, a new invasive tephritid species in Tanzania. *Journal of Economic Entomology* 103, 70–76 (2010).
51. URT. Morogoro Region Social-Economic Profile, 2020. In United Republic of Tanzania. [https://morogoro.go.tz/storage/app/media/uploaded-files/MOROGORO REGIONAL SOCIO-ECONOMIC PROFILE REPORT 2022-1.pdf](https://morogoro.go.tz/storage/app/media/uploaded-files/MOROGORO_REGIONAL_SOCIO-ECONOMIC_PROFILE_REPORT_2022-1.pdf) (2022).
52. Virgilio, M., White, I. & De Meyer, M. A set of multi-entry identification keys to African frugivorous flies (Diptera, Tephritidae). *ZooKeys* 428, 97–108 (2014).
53. Colin, C. A. & Pravin, T. Regression analysis of count data, Second edition. In *Regression Analysis of Count Data, Second Edition*. Cambridge University Press (2013).
54. Liang, K. Y. & Zeger, S. L. Longitudinal data analysis using generalized linear models. *Biometrika* 73, 13–22 (1986).
55. Mancl, L. A. & DeRouen, T. A. A covariance estimator for GEE with improved small-sample properties. *Biometrics* 57, 126–134 (2001).
56. Benjamini, Y. & Hochberg, Y. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Series B: Statistical Methodology* 57, 289–300 (1995).
57. Holm, S. A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics* 6, 65–70 (1979).
58. Hersbach, H. et al. ERA5 hourly data on single levels from 1940 to present. <https://cds.climate.copernicus.eu/datasets/reanalysis-era5-single-levels?tab=overview> (2018).
59. Zippenfenig, P. Open-Meteo.com Weather API - Astrophysics Data System. [10.5281/zenodo.7973572](https://doi.org/10.5281/zenodo.7973572) (2024).

60. Harris, C. R. et al. Array programming with NumPy. *Nature* 585, 357–362 (2020).
61. Hunter, J. D. Matplotlib: A 2D graphics environment. *Computing in Science and Engineering* 9, 90–95 (2007).
62. McKinney, W. Data Structures for Statistical Computing in Python. *SciPy* 445, 56–61 (2010).
63. Seabold, S. & Perktold, J. Statsmodels: Econometric and Statistical Modeling with Python. *SciPy* 7, 92–96 (2010).
64. Virtanen, P. et al. Author Correction: SciPy 1.0: fundamental algorithms for scientific computing in Python. *Nature Methods* 17, 352 (2020).
65. Aluja, M. & Mangan, R. L. Fruit fly (Diptera: Tephritidae) host status determination: critical conceptual, methodological, and regulatory considerations. *Annual Review of Entomology* 53, 473–502 (2008).
66. Bora, D. S., Deka, B. & Sen, A. Host plant selection by larvae of mugs silk moth *Antheraea assamensis* and the role of antennae and maxillary pulpi. *Journal of Insect Science* 13, 52 (2013).
67. Farooq, M., Baig, S., Honey, S. F., Bajwa, B. E., Fazlullah & Shah, I. H. Evaluation of host susceptibility, preference and offspring performance of *Zeugodacus cucurbitae* (Coquillett) (Diptera: Tephritidae) on different hosts. *International Journal of Tropical Insect Science* 40, 93–99 (2020).
68. Muhammad Ahmad, T. et al. Preference and performance of peach fruit fly (*Bactrocera zonata*) and Melon fruit fly (*Bactrocera cucurbitae*) under laboratory conditions. *Saudi Journal of Biological Sciences* 20, 2402–2408 (2022).
69. Ghodekar, K. S., Yendrembam, K. D., Sonawane, V. K., Longkumer, I. Y. & Ibrahim, M. M. Biology and development of the melon fruit fly, *Zeugodacus cucurbitae* (Coq.), on various cucurbit hosts. *New Zealand Journal of Crop and Horticultural Science* 53, 2603–2618 (2025).
70. Lima, I. S. & Howse, P. E. Diurnal activity and sexual maturation of the South American fruit fly (Diptera: tephritidae) in the laboratory. *Anais Da Sociedade Entomológica Do Brasil* 26, 299–308 (1997).
71. Li, J. et al. Age-Stage, Two-Sex Life Table, Oviposition Rhythms of *Zeugodacus cucurbitae* and *Zeugodacus tau*. *Journal of Applied Entomology* 150, 265–276 (2025).
72. Scolari, F., Valerio, F., Benelli, G., Papadopoulos, N. T. & Vaníčková, L. Tephritid fruit fly semiochemicals: Current knowledge and future perspectives. *Insects* 12, 408 (2021).

- 669 73. Manrakhan, A. & Lux, S. A. Diel and lifetime patterns of feeding and reproductive
670 activities of three African fruit flies, *Ceratitis cosyra*, *C. fasciventris* and *C. capitata*
671 (Diptera: Tephritidae), in semi-field cages of different spatial scales. *African*
672 *Entomology* 17, 8–22 (2009).
- 673 74. Bwire, P. M. et al. Impact of Agroecological Protection Practices Against Cucurbit
674 Infesting Fruit Flies (Diptera: Tephritidae) in Morogoro, Tanzania. *Journal of Applied*
675 *Entomology* 149, 1455–1466 (2025).

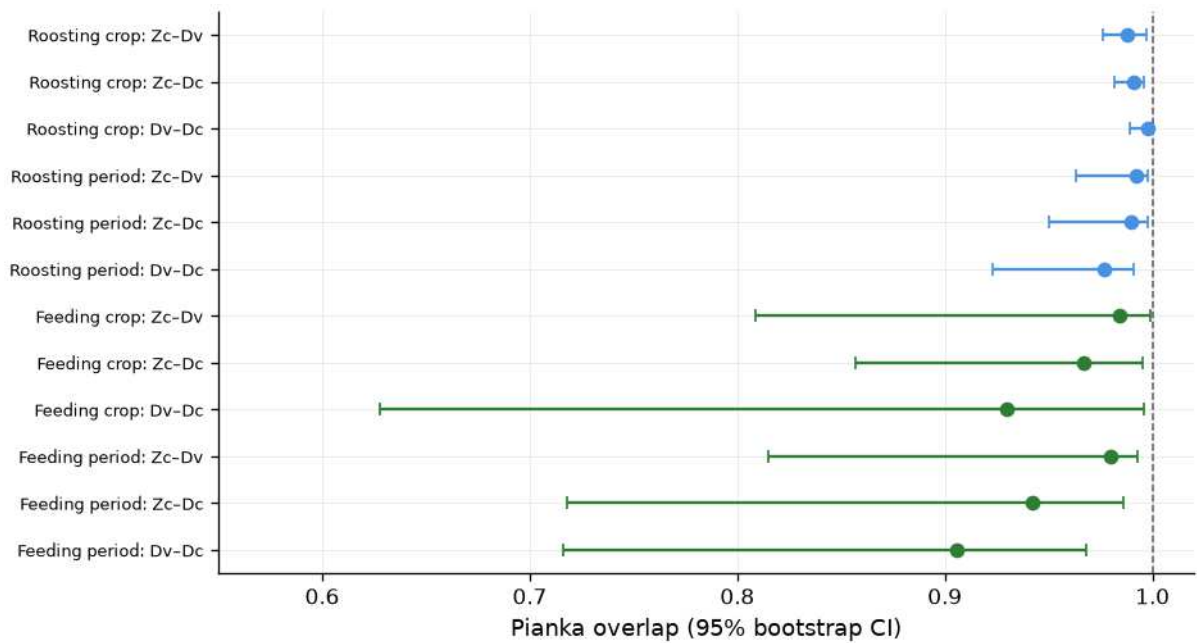
681 **Supplementary figures**



682

683 **Supplementary Fig. S1.** Observed crop-position use across daytime periods. Heat maps show
684 observed mean counts per 30-min record for feeding, oviposition, and roosting across *C.*
685 *lanatus*, *C. maxima*, and *C. sativus* for each species and daytime period. Colour scales are
686 shared within each behaviour but not across behaviours. The values are descriptive; formal
687 inference is summarized in Fig. 9.

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690 **Supplementary Fig. S2.** Interspecific overlap in crop-position and daytime-period use.
 691 Pairwise Pianka overlap indices summarize similarity in proportional crop-position and
 692 daytime-period use among species. Values approaching 1 indicate greater similarity in
 693 observed proportional use. These indices describe similarity and do not test competition or
 694 behavioural mechanisms.