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Temporal activity patterns of predators and prey across broad geographic scales

Running title: Activity patterns of predator and prey

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Data Accessibility

We commit to providing all the necessary data and R code required for reproduction of our analyses reported in this article (data uploaded to Dryad, and a DOI cited in the final version of the text).

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Lay summary

Predators align their hunting effort with the daily activity patterns of prey. Using large citizen-science datasets, we show that bird-eating raptors hunt more at times when songbirds are active rather than when they are vulnerable. This behaviour is consistent over broader scales, with the same patterns observed for closely-related predators across two continents. Our finding provides insight into the ongoing arms race between predators and their prey.

Abstract

Predators and prey are locked in an evolutionary arms race that shapes their behaviour and life history. Predators target prey vulnerabilities to maximise hunting success, while prey trade-off foraging against predation avoidance. Though studies have demonstrated how predation risk can alter how prey allocate daily foraging effort, little work has considered the implications of this temporal component of behaviour from a predator's perspective, or assessed its influence on broad-scale predator-prey interactions. We develop a method to compare daily activity patterns of avian predators and prey using data from two large citizen science datasets collected on different continents. Our analyses reveal evidence for convergent daily hunting strategies across avian predators, with distinct differences according to prey type. By comparing predator data with correspondent data from songbirds, our study suggests that predators (*Accipiters*) specialised to hunt songbirds match the activity patterns of their prey species. These results indicate predators have evolved common temporal hunting strategies to exploit temporal patterns in prey behaviour.

Keywords: Hunting strategies, foraging behaviour, activity patterns, predator-prey interactions

Introduction

Predators are a major selective force shaping the morphology, behaviour and life history of prey (Clements et al., 2016; Lima and Dill, 1990; Reznick and Endler, 1982; Sih, 1980). Through the act of foraging (hunting), predators themselves also drive prey adaptations – including changes in behaviour, that can subsequently make hunting more challenging (Gosler et al., 1995; Palkovacs and Post, 2008; Sih, 1984; Tambling et al., 2015). We therefore expect that predators should exploit fundamental limitations in their prey – such as to target opportunities where prey have limited ability to evolve counter-adaptations. Though predator-prey dynamics have been extensively studied for decades (Abrams, 2000), there is still little information available about foraging strategies of predators (Lima, 2002). For example, we don't fully know when predators invest most effort in hunting. Characterising predator hunting behaviour, such as when they allocate effort, and linking this to prey behaviour, is an important step towards gaining a better understanding of predator-prey co-evolution (Dawkins and Krebs, 1979).

Prey behavioural responses to predation have been widely explored from both theoretical and empirical perspectives (Lima, 1998; Lima and Dill, 1990; Sih, 1984; Sih and McCarthy, 2002). Studies have demonstrated how prey can trade-off predation risk against other benefits when making behavioural decisions (Lima and Dill, 1990), and adjust behaviour according to the level of risk (Helfman, 1989; Kotler et al., 2010). As predator-prey systems universally show temporal variation in predation risk (over daily (Metcalfe and Ure, 1995), lunar (Prugh and Golden, 2014) or seasonal (Sperry et al., 2008) cycles), many investigations of prey responses to predation risk have sought to understand the temporal aspect of anti-predator behaviour (Lima and Bednekoff, 1999b; Mirza et al., 2006). For example, theoretical studies have modelled the temporal strategies that songbirds can use to balance predation against starvation risk (Houston and Mcnamara, 1993; Lima, 1986; Mcnamara et al., 1994) (reviewed by Brodin

(2007)). These models predict that prey should use a bimodal feeding routine, with temporal peaks in feeding activity at dawn (to counter loss of energy stores overnight) and dusk (to avoid starving the following night). Empirical studies of wild songbirds partly support the prediction of models on bimodal feeding routines, showing that prey use temporally dynamic feeding strategies to (presumably) minimise predation risk (Macleod et al., 2005a; van der Veen, 1999) (though work by Bonter *et al.* (2013) refutes bimodal feeding). Recent empirical evidence points to the presence of a two-part foraging strategy; prey feed less and move more for the first half of the day whilst searching for food patches (Farine and Lang, 2013), then shift to exploiting (higher feeding rates) discovered patches later in the day (Bonter et al., 2013; Macleod et al., 2005b). Results from optimal sampling experiments support the presence of this two-part behaviour, as a discovery-exploitation strategy would function to find and consume the most profitable food patches (Krebs et al., 1978). Together, these findings demonstrate that prey species can change their foraging behaviour over the course of a day based on the presence of predators and starvation risk, and highlights the importance of the temporal component of their behaviour (Ferrari and Chivers, 2009; Lima and Bednekoff, 1999b; Matassa and Trussell, 2014).

Despite being well studied in avian prey (Ferrari et al., 2010; Kronfeld-Schor and Dayan, 2003; Matassa and Trussell, 2014; Mirza et al., 2006), our understanding of the temporal component of behaviour for their predators remain incomplete (Ferrari and Chivers, 2009). Two previous studies have qualitatively investigated temporal patterns of predator behaviour by using data from individually radio-tagged hawks in Europe (Newton, 2010) and North America (Roth II and Lima, 2007). The results of these studies differ; Newton (2010) reports that Eurasian sparrowhawk, *Accipiter nisus*, show a morning peak of activity, while Roth II and Lima (2007) found that Cooper's hawk, *Accipiter cooperii*, exhibited bimodal peaks of activity at sunrise and sunset, and Sharp-shinned hawk, *Accipiter striatus* had low morning activity, higher activity during the day, and a pre-sunset peak. In both studies however, the apparent consensus was that timing of predator behaviour appeared to be matched to the activity of prey. Though these tracking studies have improved our understanding of the temporal component of predator behaviour, the effort required for each capture of an individual for tagging limits the sample size (and thus spatial range) available to draw from. As a result, research has not fully explored the temporal behaviour of predators on wider population levels. Without a large-scale methodological technique for collecting directly comparable data across species and geographic ranges, we are unable to fully assess broad-scale interactions between predators and prey, limiting our ability to generate and test hypotheses about predator temporal hunting strategies.

Here, we develop a broad-scale approach to quantify the temporal activity profile of predators, and to relate these patterns to the temporal profiles of prey activity. We utilise two large citizen-science datasets of bird observations across the continental United States (herein North America) and Great Britain/Ireland to assess when avian predators allocate time to hunting. These datasets comprise ‘checklists’ of all the bird species observed during a timed observation period. We simplify checklists to focus on 16 species, chosen as the most common avian predators in each region, and their common avian prey species. As focal predators, we included species from three genera (*Accipiter*, *Falco* and *Buteo*), which characterise three functionally different predator groups. Accipiters are specialised in hunting almost exclusively birds (Gotmark and Post, 1996), whereas *Falco* and *Buteo* species have different primary prey types (predominantly mammals (Graham et al., 1995) and insects (Korpimäki, 1985)), and are included for comparative purposes. We then estimate the activity profiles of predator species alongside those of their prey.

We hypothesise that diurnal predators could employ one of three hunting strategies for allocating hunting effort to exploit the temporal limitations of prey. Their strategies could target the times of the day when prey are most vulnerable due to (i) **movement activity** (when having to search for new food resources), (ii) **feeding** (when they have to accumulate fat), or (iii) **the**

environment (when they are least able to detect predators). Under a strategy that matches prey activity (i), predators should intensify hunting effort at times when prey are searching for new food resources, as the increased movement of prey increases the chance of encounter (Banks et al., 2000). Under a strategy that matches prey feeding (ii), predators should hunt more at times when prey are least vigilant, or least able to escape predators. Higher feeding rates result in decreased vigilance (Lima and Bednekoff, 1999a), and decreased manoeuvrability as a result of fat accumulation. From previous studies of songbirds, such feeding rates are usually observed to be constant or slowly increasing following dawn, sometimes with peaks shortly before sunset (Bonter et al., 2013; Brittingham and Temple, 1992), while body mass steadily increases over the day (and is thus greatest in the late afternoon) (Macleod et al., 2005b; Moiron et al., 2018). Finally, under a strategy that matches the environment (iii), predators should hunt most when the environment increases the chances of hunting success. Specifically, we hypothesise that low light conditions (during dusk or dawn) could impair the ability of prey to detect distant predators, thereby reducing the effectiveness of prey vigilance, whilst increasing the success rate of ambushes by diurnal predators that possess greater visual acuity (Heurich et al., 2016; Klinka and Reimchen, 2009; Lima, 1988). These three hypotheses represent quite different potential behavioural patterns that should have distinct temporal profiles. By identifying common temporal patterns within taxa and across countries on two different continents, and contrasting patterns between predator species according to prey type, we generate new insights into behavioural strategies of the predator-prey arms race.

Methods

Data Collection

To source behavioural data for our analyses, we compiled datasets from two large publicly-accessible databases: BirdTrack (Ireland/SOC/WOS, 2017. Available at: www.birdtrack.net) (collected across Great Britain/Ireland); and eBird (Sullivan et al., 2009) (collected globally but here using data from the continental United States – herein North America). Both are citizen science projects where volunteers submit observations (in the form of checklists) of bird species, which are saved to a central database. In order to be able to account for varying hourly observer effort across the day, we only included records that were submitted with a start and stop time (i.e. had a checklist period). This start and stop time of each record was used to determine its observation period, and calculate hourly observation rates.

We created unique datasets for each focal species (Table 1). First, we generated a complete list of all checklists available in the databases (BirdTrack: 2004 to 2016, eBird: 2002 to 2012). We then created a record that summarised each checklist in terms of the presence or absence of the focal species. Duplicate checklist records from a group of observers were excluded, retaining only the primary observer. Checklist count data per species was reduced to 1 for presence and 0 for absence because we aimed to test activity, and the probability of observing the species as active was more informative than the number of individuals observed. We then trimmed each dataset to omit records with exceptionally long (>3 hours) or short (identical start/stop times) observation periods. Because we were interested in resolving temporal activity patterns, long observation periods were uninformative as our binning procedure (detailed below) means they contribute equally to most hours and therefore even out to have no effect on the results. Conversely, observations with the same start/stop time were likely to have been submitted as anecdotal sightings, which might be more likely to occur for uncommon species and thus could introduce a positively-biased observation probability for predator species. Species were selected based on being widespread across the majority of each continent and being predominantly present year-round. Equal geographic distribution of all predator and prey species across study areas was verified by plotting the location of all observations used in the analyses.

Time Correction

To account for latitudinal differences in sunrise and sunset times, we modified the data to represent the time relative to the local sunrise and sunset times. Using the 'suncalc' function in the RAtmosphere package (Biavati, 2014) in R, we computed accurate local sunrise and sunset times at the location and date each observation. Using these location-specific sunrise/sunset times, we then calculated the mean monthly sunrise and sunset times across all observations, yielding a single value for the dawn and dusk of every month (separately for each data set). We then shifted all of the observation start and end times to have a common sunrise (for morning observations) and sunset (for afternoon observations) time, and avoiding situations where an observation that, at a given location, was made after sunrise (e.g. at 6:15am where sunrise at that location was 6am) ended up being modelled as occurring before sunrise (e.g. if the mean sunrise time was 6:30am, then the observation was shifted to 6:45am). That is, the start and end times were shifted to be correct relative to the mean monthly sunrise and sunset times, rather than using the raw observation time (which is only correct relative to the local sunrise and sunset times).

Hourly Binning

Because records represented the binary presence of the focal species, but could span more than one hourly period, we assigned sightings proportionately to the amount of time the observation period fell in each hourly period. For example, a record containing a sparrowhawk that started at 09h40 and finished at 11h00 would contribute 0.25 of a sighting for the hour 09h00 (09h40-10h00 – or one quarter of the total observation period), and 0.75 for the hour 10h00 (10h00-11h00, three quarters of the total observation period). We then calculated the sum of these (fractional) observations from each hour. This hourly partitioning was conducted independently for each record of each species in the datasets.

The number of sightings of a species in each hour is likely to be a function of not only that species' activity profile, but also observer effort, which could vary across the time of day. In order to correct for this, we used the complete set of trimmed records for the focal species, including both presence and absence records to generate a measure of total observer effort across time. First, we calculated how much of each hour the observer was active. For example, a (time-corrected) record from 09h40 to 11h00 would yield an effort value of 0.33 for 09h00 (09h40-10h00 – one third of the hour), and an effort value of 1.0 for 10h00 (10h00-11h00 – the full hour). We then divided the hourly sum of the number of observations by the hourly sum of the observer effort to generate the probability of sighting the focal species per hour of observer effort (see sample of this methodological process in Figure S1 of Supplementary information). We interpret this probability as akin to an activity profile, as species have a higher/lower probability of being observed at higher/lower levels of movement activity – this has been shown in previous work where individual movement between sites correlates with higher detection rates (Farine and Lang, 2013). Because our hypotheses are based on time of day, which changes over the year, we calculated these probabilities separately for each month of the year.

Permutation Test

We used a permutation test to identify times of day in which observations of the focal species differed from the expectation by chance. Because our measure of interest was the probability of observing the focal species in a given hour, our aim was to generate a null distribution of the hourly probability of observation. We constructed the permutation test by randomly allocating the presence records for the focal species across all records in the dataset. That is, our input dataset contained one row representing each unique observation record, with a column containing the information on whether the focal species was observed in that record or not (a binary 0 or 1). Our permutation test shuffled this ‘observed’ column (thus maintaining both the number of observations of the focal species and the observer effort in time constant). After performing this re-allocation of presence data, we re-calculated the probability of sighting the focal species per hour of observation effort (as above) for each hour. We repeated this process 1000 times for each focal species, and extracted the 95% range of the distribution for each hour.

This 95% range of random sampling data is shown by the grey polygons in Figure 1, and Figures S2-S17.

Log-Ratio Differences from Random

To make the non-random patterns in the activity profiles of species more directly comparable, we extracted the hours of the day (for each month) in which the observed probability was outside the range of permuted data. When the observed probability was above the 97.5% quantile, we plotted the area using a red polygon. When below the 2.5% quantile, we plotted the area as a blue polygon. We then generated a figure by plotting these monthly polygons overlaid in a stack per species. Because the ability for observations to differ from random changes at different baseline probabilities (i.e. the largest differences are possible at 0.5), we plotted these values on the y-axis as the log of the ratio between the observed and upper (for above) or lower (for below) 95% quantile. Because of seasonal changes in the mean sunrise and sunset times, we plotted all of the data relative to the mean sunrise and sunset time across the entire data (using the same procedure as described above to shift each month's polygons). This allowed us to combine the observation probability curves for each species of predators and prey in North America (Figure 2a) and Great Britain/Ireland (Figure 2b) plotted on a common temporal axis without any effects of geographical or seasonal differences in day length, and removing any effects of seasonal differences in observability of species arising due to their migration outside of the area covered by our datasets.

Predictive Modelling

To test our 'prey activity-matching' hypothesis – how closely the daily activity pattern of different predators matches the daily activity pattern of prey, we developed a predictive model using a Gaussian process framework (Mann et al., 2011; Rasmussen, 2006). The predictive model enables us to quantitatively test how well the inferred activity profile for prey species predicts the inferred activity profile for predator species. We used all but one prey species from each continent as training data to fit a Gaussian process model describing the activity profiles (the non-included species was chosen by selecting a species with a large geographical range; the results of our analyses were not affected by this choice). The fitted model describes a probability distribution over possible activity profiles, and is specified by a mean profile (the average amount of activity at each time) and a covariance matrix (the temporal correlations in activity). The mean profile was estimated by the sample mean of the training data, while the covariance matrix was estimated using shrinkage estimation (Schäfer and Strimmer, 2005). We then evaluated how well this model predicted the activity profile of each predator found on the same continent (the predictive probability of the predator profiles). We also evaluated the predictive probability for the remaining prey species as a baseline for each dataset (i.e. how well do prey species predict other prey species). To determine how much this prediction can be attributed to the precise temporal pattern of the activity profile, we compared the predictive power of the model trained on real data (using the original activity profiles) with a model trained on a set of all 18 possible time-shifted copies of the original training data (where the temporal position was shifted in time by 0 to 17 hours, preserving the overall shape of each activity profile and maintaining the same temporal autocorrelation in both datasets). We then plotted the resulting difference (reported as Log_2 information gain). This difference shows how much more or less informative real data was than the shifted data. If predators match the activity of prey, then we expect that the prey patterns of activity should predict the activity patterns of their predators. Using bootstrap resampling on the 12 months of activity profiles for each test species and recalculating the information gain from these resampled data, we created 95% confidence intervals on the values of the information gain (using the 0.025 and 0.975 quantiles). Bootstrap resampling also provides an estimate of the p-value for each information gain, on the null hypothesis that information gain is 0. We report the information gain for each species separately, providing a quantitative test of the temporal difference in the activity profiles of predators and prey (Figure 3). We further explored how predictive power varied with the amount of shift, by plotting the increase/decrease in information for every possible iteration of hourly shift used (Figures S18-S19). All analyses were carried out using *R* (R Development Core team, 2010).

Results

Our primary aim was to determine when avian predators allocate time to hunting, and how these activity patterns relate to the behavioural patterns of prey species. Hourly binning and permutation test analyses revealed consistent temporal variation in the probability of sighting focal species over the course of the day (black line, Figure 1, Figures S1-S17). We found that all analysed prey bird species from both North America (Figure 2a) and Great Britain/Ireland (Figure 2b) showed similar daily patterns of activity. These are marked by higher than random activity in the morning period (dawn to midday), peaking at approximately 08h00, and often declining in the afternoon onwards – consistent with empirical data collected by Farine & Lang (2013). While the above/below random patterns were consistent among all prey from each continent, the overall observation probability for prey species reflected variations in abundance, being higher for common species such great tit, chaffinch, house sparrow and American goldfinch, but lower for less common species like nuthatch and dark-eyed junco. There was also variance in the monthly observability of many prey species, with less pronounced daily patterns observed from May to August for North American species (notably during the autumn migration of dark-eyed junco – Figure S9), and from November to February for species from Great Britain/Ireland (detailed monthly prey results can be found in Figures S6-S9 and S13-S17). Migration is apparent by the reduction in the probability of observations across the entire daytime period in months when the species has migrated.

For predators, daily patterns of behaviour appeared to vary according to the type of prey specialisation, with species' activity profiles differing more across genera than between continents (Figure 2). *Accipiter* species (*A. nisus*, *A. cooperii* and *A. striatus*) showed a higher than random period of activity in the late morning. *Buteo* species (*B. buteo* and *B. jamaicensis*) showed a later and more extended period of higher than random activity, with a sharp increase before the peak, and a gradual decrease after it. Both *Falco* species (*F. sparverius* and *F. tinnunculus*) – much like the *Buteo* species – showed an extended period of higher than random activity around midday, but with a bimodal pattern: with one peak occurring in the middle of the day and another in the mid-afternoon. The general activity patterns of predators remained consistent between months. *A. striatus*, which is less abundant in North America throughout its migration period, showed less pronounced activity patterns during Autumn, but still retained consistent activity patterns for the rest of the year (detailed monthly predator results can be found in Figures S2-S5 and S10-S12). Overall, the daily activity profiles of *Accipiter* species on both continents appeared closely time-matched to the morning activity peak of their prey (Figure 2). In contrast, the activity of *Falco* and *Buteo* species appeared to be less closely matched to that of the prey bird species, as their activity peaked closer to the middle of the day.

Our predictive modelling statistically showed how closely predator behaviour is matched to prey. Prey bird species had the greatest power when predicting the daily activity profile of the one remaining prey species per continent not included in the training data, *P. domesticus* ($P \leq 0.001$) and *F. coelebs* ($P \leq 0.001$), suggesting that prey species have generally similar daily patterns of activity. In line with our initial results of Figure 2, the prey bird species were significantly better than the shifted data in predicting the daily activity profiles of two of the *Accipiter* predators, *A. nisus* ($P=0.004$) and *A. cooperii* ($P=0.007$). An additional posthoc analysis examining the effect of each hour of timeshift suggested that *Accipiter* predators foraged predominantly at the same time as prey, but also up to two hours after the peak in prey activity (Figures S18-19). Comparatively, the activity profiles of three out of four *Falco* and *Buteo* predator species were significantly less predicted by the prey bird species than by the shifted data; *B. jamaicensis* ($P \leq 0.001$), *F. tinnunculus* ($P \leq 0.001$) and *B. buteo* ($P \leq 0.001$). Our analysis suggests that the pattern of similarities between specialist avian predators and their avian prey is unlikely to have arisen simply by chance.

Discussion

We found that predators exhibit clear peaks in their activity over the course of a day. These activity patterns varied according to predator ecology. *Accipiter* species, which primarily hunt birds, were most active during the mid-morning, whilst all prey bird species analysed were also most active in the morning period. By contrast, *Falco* and *Buteo* species (largely mammal and insect hunters) were most active during the middle of the day. While these results cannot conclusively demonstrate the directionality of the relationship, our findings strongly suggest that predators which are most specialised to hunt birds (*Accipiter* spp.) closely align their activity profile with the time of day that their prey are most active. By contrast, we find little evidence to support the hypotheses that predators are targeting periods of the day in which prey birds may be more vulnerable due to the environment (e.g. low light levels at dawn and dusk) or alternatively are hunting when prey birds are most vulnerable due to their foraging needs (in the evening). The similarity of activity profiles from data collected on two continents, and across a broad range of species, suggests that patterns of highest activity during the morning could represent a convergent equilibrium between predator and prey behaviour.

Our ‘prey activity-matching’ hypothesis posits that predators should allocate their hunting effort to times of the day when their prey are most active. From our results on the temporal behaviour of prey birds from both continents, this period of highest prey activity is in the early-to-mid morning period. This finding is supported by previous studies on prey species, which show that prey exhibit the highest movement activity in the first half of the day (Farine and Lang, 2013). For the prey bird species we studied, the higher rates of movement in the morning could be because they are acquiring information about the state of their environment, such as where the best food sources are (Farine and Lang, 2013; Krebs et al., 1978). Further, searching in the morning incurs less starvation risk than later in the day (Bonter et al., 2013) (because a bird that fails to find food in the morning still has time to find food later in the day). For predators, hunting when prey are on the move should be more efficient because prey individuals are more likely to arrive in the target area of the predator with no information about its presence. Predators also likely benefit from improved prey detection, as they can eavesdrop on vocalisations used by searching prey (such as recruitment calls - Suzuki, 2012)). The observed temporal pattern of morning activity in accipiters is consistent with the results of a qualitative study by Newton (2010) where radio-tracked *A. nisus* individuals were found to have a higher mean number of flight movements in the first half of the day. Our results are also in line with theoretical work on foraging games, which indicate that the foraging strategies of prey shape their basic activity pattern, and the evolutionarily stable strategy for activity patterns of predators should match that of prey (Kotler et al., 2002). By contrast, predators that are less specialised to hunt avian prey (such as *Buteo* and *Falco* species) appear to be less closely aligned to temporal activity of songbirds. We note that while *F. sparverius* do occasionally hunt birds (potentially more in northerly populations during winter), these represent a small fraction (<10%) of the total number of prey items in their diet (Sherrod, 1978). Instead, *Buteo* and *Falco* species tended to hunt most around midday, which is when key prey such as small mammals and insects are likely to be most active (Rijnsdorp et al., 1981).

Our results (Figure 2) give no apparent support to two alternative hypotheses relating to how predators might hunt when their prey are most vulnerable as a result of other prey behavioural strategies, or as result of the environment. The first of these is perhaps best linked to a ‘behavioural vulnerability’ that has been hypothesised elsewhere and relates to feeding; prey are more at risk of being captured by predators when they have high levels of body fat (Metcalfe and Ure, 1995; van der Veen, 1999). Studies have shown that when *A. nisus* became re-established in the UK, resident prey species decreased the body mass they carried (Gosler et al., 1995). Further studies have since shown that when predators are present, prey will also alter their feeding strategies to delay carrying body fat until later in the day (Macleod et al., 2005b). Models have assumed that prey species have decreased manoeuvrability due to higher mass or decreased vigilance as a consequence of having to increase feeding rates as the day progresses, which accipiters could target by hunting in the afternoon. However, our results suggest that these predators are actually less likely to be observed in the afternoon and evening than expected by chance. This could be because foraging strategies of prey make them less vulnerable in the evening (e.g. they can increase vigilance if at less risk of starving) or more vulnerable in the morning (e.g. if they have higher rates of movement and reduced vigilance while replenishing energy reserves lost overnight) than previously thought.

The second vulnerability that predators could target is the reduced visibility in the morning and evening. With their high visual acuity, predators could presumably spot and target prey in low light conditions, whilst making themselves more difficult to detect. Under this ‘environmental vulnerability’ hypothesis, predators should allocate the most hunting effort during dawn and dusk. This hypothesis is supported by evidence that indicates prey species are responsive to indirect cues of higher predation risk. For example, prey species will often be more alert for nocturnal predators on nights with low visibility (e.g. a new moon - Fanson, 2010). Our results (Figure 2), however, suggest that avian predators do not exclusively target times of low light: out of all predators assessed in our study, no species ever exhibited its highest hunting activity in both dawn and dusk. Though *A. cooperii* was occasionally observed before sunrise (which could signify some low light hunting), in general, rather than being earlier, the morning activity pattern of accipiters was slightly delayed relative to prey species (Figure 2, Figures S18-19). This broad-scale delay in activity mirrors the findings of a fine scale tracking study of North American accipiters, where the lag in activity was longer for *A. striatus* than *A. cooperii* (Roth II and Lima, 2007). Roth and Lima (2007) suggest that the smaller-bodied *A. striatus* are at high risk of intraguild predation risk from owls around sunrise and sunset, and the lag they observed signals the avoidance of overlap with such superpredators. One alternative reason for this delay could be that the avian predators we studied are actually unable to detect prey in low light conditions (or are less capable of detecting prey than prey are at detecting predators), and therefore do not benefit from hunting during this time. The morphological differences between the eyes of nocturnal and diurnal predators have recently been well described (Jones et al., 2007). Many prey bird species have eyes adapted for visual sensitivity (the ability to spot movement) in twilight conditions. By contrast, predators are faced with a trade-off between visual sensitivity in twilight and visual acuity (the ability to differentiate objects) in daylight (Mitkus, 2015), and appear to have not countered the twilight adaptations of their prey. While the reduced predator activity in twilight could alternatively be explained by observers themselves having reduced acuity (and thus reduced detection range) in near-darkness, recent research suggests that humans have cognitive adaptations that improve perception during twilight hours (Cordani et al., 2018). From these studies, we can assume that if light levels are sufficient for diurnal predators to hunt, then they are also sufficient for observers and for prey to see them. Work on nocturnal animals highlights how variation in acuity impacts predator-prey dynamics (Prugh and Golden, 2014), but as of yet, the absolute ability for diurnal predators to detect prey in low light is unknown. There is much that could be learnt by quantifying in detail the sensitivity and acuity of predators, prey, and human observers under different light conditions, and using these data to model some of the evolutionary trade-offs faced by predators (e.g. increasing visual sensitivity versus maximising visual acuity).

A prominent feature of our results is the similarities of activity profiles of species with similar life histories across two continents. These patterns are detectable thanks to the large amounts of data made available by birdwatchers recording their observations. These observational datasets allow us to take a large-scale approach, complementing fine-scale studies of predator behaviour (Roth II and Lima, 2007). While fine-scale tracking studies can inform us about individual variation and between-sex/age differences (Newton, 2010), large scale approaches provide insight into behavioural dynamics at the population-level. However, observational data also have some limitations. Chiefly, our analyses rest upon the assumption that predators are more likely to be sighted when they are more active in hunting. An antagonistic interpretation of our results is that predators might actually be least active in hunting when sighted most commonly, which could be the case for 'sit-and-wait' predators that hunt by remaining in a fixed position to ambush prey (Jaksić and Carothers, 1985). These ambush predators would instead be observed most often when moving between ambush sites (and not when actually hunting). If this were the case, it could support the hypothesis that predators are indeed hunting when prey are most vulnerable (for example in the afternoon when carrying the most body fat). However, our assumed link between observability and hunting is supported by the similar result reported in a smaller-scale study of real predator hunting activity based on tracking individual birds (Newton, 2010). Moreover, several empirical studies have found no evidence for decreased manoeuvrability (and increased vulnerability) of avian prey species carrying higher levels of body fat (Kullberg, 1998; Veasey et al., 1998), which, alongside our findings, suggests that prey mass cycles are unlikely to solely govern the daily hunting strategies of raptors. Greater insight could be gained by comparing ambush and non-ambush predators of common prey, and modelling the economic value of different predator strategies as a function of prey behaviour – for example, by testing if the chance of a predator being spotted by prey while moving is higher or lower when prey species also move more. We posit that such hunting costs will be lower when prey are on the move, as the information and certainty of the predators' location (from the perspective of the prey individuals) becomes outdated more quickly (Sih, 1984). Finally, a limitation of studies that use methodologies such as ours is that the results are based on correlational data. We hope that natural experiments, such as the return of sparrowhawks into the UK after being nearly extirpated by DDT (Gosler et al., 1995), will provide conclusive support for our data, and allow for further empirical tests of our findings.

Conclusion

While predator-prey dynamics are thought to be reciprocally driven by continuously evolving behaviours, we have found consistent patterns of behaviour in species from different continents. Our results suggest a possible convergent state of equilibrium in the temporal behaviour of predators and their key prey. As increasing quantities of observational data are collected by citizen scientists in the coming years, this method for calculating activity could prove to be a powerful way to further assess the dynamics of behavioural interactions between predator and prey, and link these processes across different temporal scales (Estes et al., 2018). Further studies could also explore whether patterns change over years, differ across habitats, vary according to climatic conditions, or even change depending on the relative abundance of predator species. While distinct peaks in non-random activity in predators are detectable, we still don’t fully understand the finer level dynamics that might be occurring within these high-activity periods. A key additional element to hunting strategies is how predators invest hunting effort spatially across their home-range. We hypothesise that predators with a large home range would be much less predictable in terms of where they might occur, and therefore could afford a more relaxed temporal strategy. More research is needed to explore the temporal and spatial dynamics of behavioural feedback cascades triggered by hunting activity of predators, particularly at the within-day level of the individual.

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Tables

Table 1: Details of data on the 16 focal species (including both predators and prey) used in the analyses. The table includes the source and number of records after subsetting by duration. The total number of checklists used (including absent records) from eBird was 2.8 million, and from BirdTrack was 0.8 million.

Common name	Latin name	Main prey type	Data source	# ‘present’ records
North American predators				
Cooper’s hawk	*Accipiter cooperii*	Birds	eBird	141,362
Sharp-shinned hawk	*Accipiter striatus*	Birds	eBird	69,364
American kestrel	*Falco sparverius*	Mammals	eBird	193,629
Red-tailed hawk	*Buteo jamaicensis*	Mammals/other	eBird	401,878
North American prey				
House sparrow	*Passer domesticus*	-	eBird	549,662
American goldfinch	*Spinus tristis*	-	eBird	739,952
Housefinch	*Haemorhous mexicanus*	-	eBird	630,384
Dark-eyed junco	*Junco hyemalis*	-	eBird	288,887
GB/IRE predators				
Sparrowhawk	*Accipiter nisus*	Birds	BirdTrack	69,998
Kestrel	*Falco tinnunculus*	Mammals	BirdTrack	136,749
Buzzard	*Buteo buteo*	Mammals/other	BirdTrack	190,790
GB/IRE prey				
Great tit	*Parus major*	-	BirdTrack	408,732
Blue tit	*Cyanistes caeruleus*	-	BirdTrack	469,748
Robin	*Erithacus rubecula*	-	BirdTrack	498,765
Chaffinch	*Fringilla coelebs*	-	BirdTrack	443,698
Nuthatch	*Sitta europaea*	-	BirdTrack	78,425

Figure legends

Figure 1: The probability of sighting a Cooper's hawk (*Accipiter cooperii*) is significantly higher in the morning than in the afternoon. Solid black line denotes observed hourly sighting probability for each calendar month. The grey-shaded polygon indicates the 95% range of the distribution of random sampling. Coloured polygons highlight where the observed probability is above (red) or below (blue) the probability of observing that species if they were observed randomly throughout the day. Vertical dashed grey lines represent the mean sunrise (left) and sunset (right) times across all of the data for each month. This plot is replicated alongside similar plots for all other focal species in Figures S2-S17.

Figure 2: Predator activity profiles match the profile of their prey, and are consistent within genus across continents. Plots of log ratio of the observed versus the upper (red) and lower (blue) quantiles of the 95% range expected by chance (see Figure 1). Each subpanel represents the data from one species, and each transparent polygon is the data from one month (thus each subpanel contains 12 red and 12 blue polygons). Dotted lines indicate mean sunrise and sunset times for dataset against which all data are plotted. Data are shown for both predators (upper rows) and prey (lower rows) for a) North American species (eBird), and b) Species from Great Britain/Ireland (BirdTrack). Predator species genera are illustrated by black outlines.

Figure 3: Predictive power of prey activity profiles is greatest when predicting the activity profile of specialist avian predators and other avian prey. Bar plot showing predictive power (Log_2 information gain) of prey species on the activity profile of one prey species and each predator species from the same continent (only species from the same datasets were used for comparisons). For North American species (a) the training data comprised *S. tristus*, *J. hyemalis*

and *H. mexicanus*. For species from Great Britain/Ireland, (b) the training data comprised *P. major*, *C. caeruleus*, *E. rubecula* and *S. europaea*. Grey bars show predictive power as information gained by using real training data compared to shifted training data (where overall shape of activity profile was maintained, but shifted in time by 0- 17 hours). Positive numbers show how much more informative real training data is compared to shifted data, when predicting the activity of the focal species (activity occurs at similar times). Negative numbers show the real training data is less informative than shifted training data (activity occurs at different times). Bootstrapping was used to create 95% confidence intervals on the values of the information gain by resampling the monthly activity profiles for each test species. P-values estimated from bootstrap evaluations denote whether the information gain was significantly different from zero (two-tailed test).

Figures

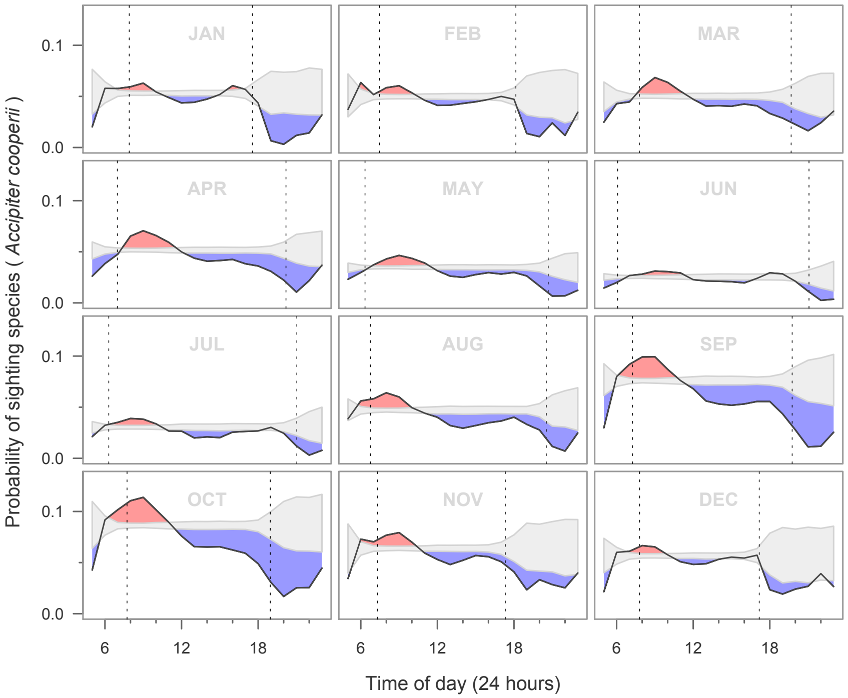

Figure 1

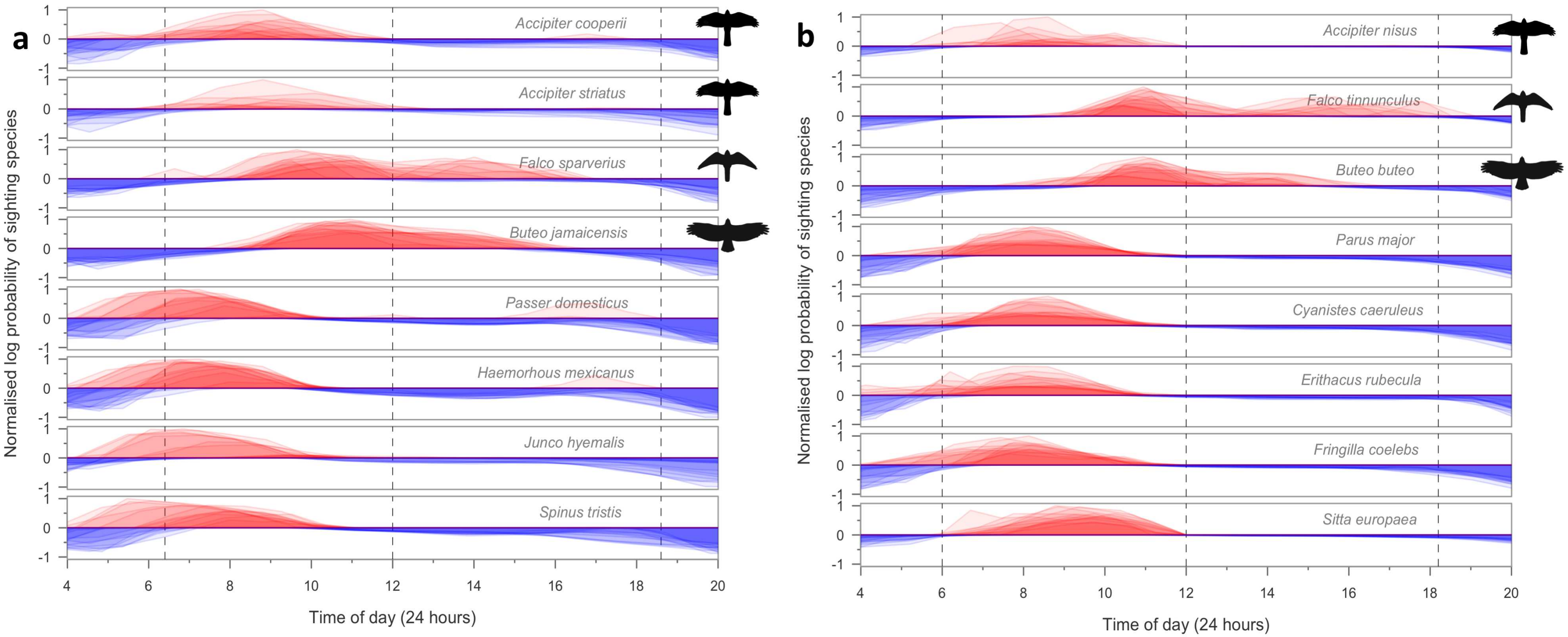
a
b
Normalised log probability of sighting species
Accipiter cooperii
Accipiter striatus
Falco sparverius
Buteo jamaicensis
Passer domesticus
Haemorhous mexicanus
Junco hyemalis
Spinus tristis
Accipiter nisus
Falco tinnunculus
Buteo buteo
Parus major
Cyanistes caeruleus
Erithacus rubecula
Fringilla coelebs
Sitta europaea
1
0
-1
4
6
8
10
12
14
16
18
20
Time of day (24 hours)

Figure 2

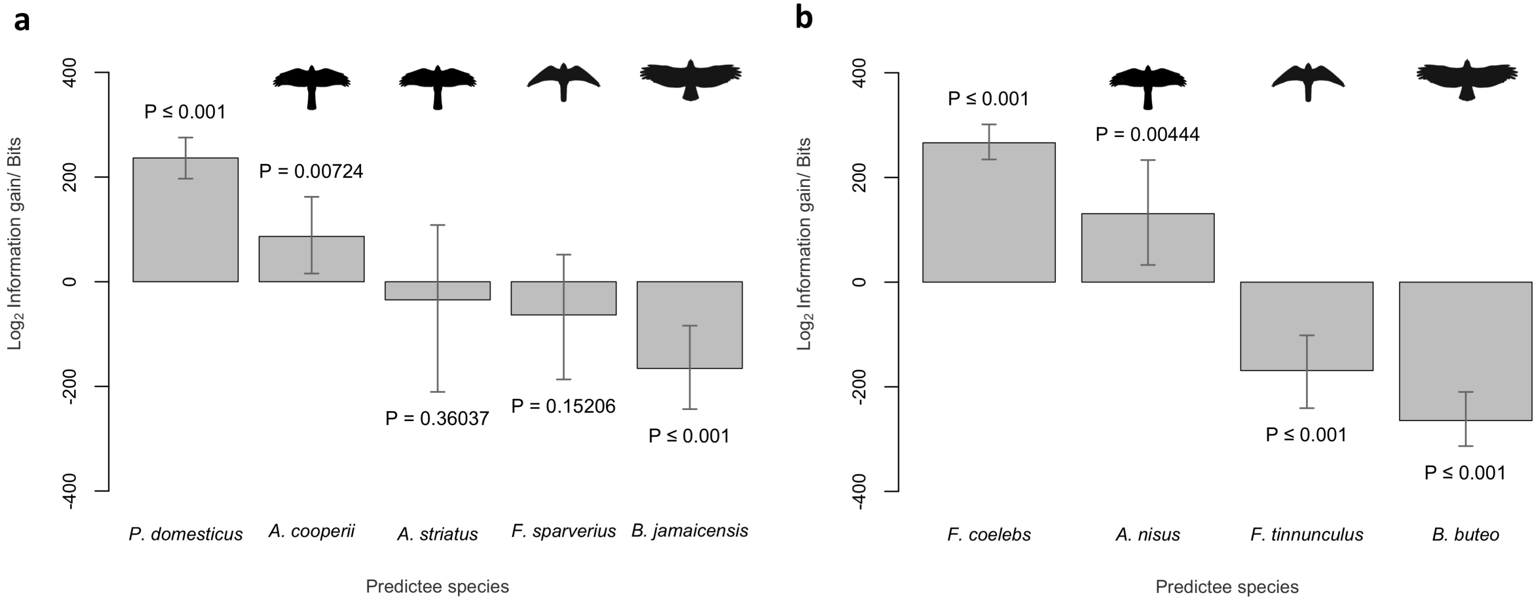
a
b
Log₂ Information gain/ Bits
400
200
0
-200
-400
P ≤ 0.001
P = 0.00724
P = 0.36037
P = 0.15206
P ≤ 0.001
P. domesticus
A. cooperii
A. striatus
F. sparverius
B. jamaicensis
Predictee species
P ≤ 0.001
P = 0.00444
P ≤ 0.001
P ≤ 0.001
F. coelebs
A. nisus
F. tinnunculus
B. buteo
Predictee species

Figure 3

Supplementary Material

Temporal activity patterns of predators and prey across broad geographic scales

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METHODOLOGY FOR NORMALISING OBSERVATION DATA

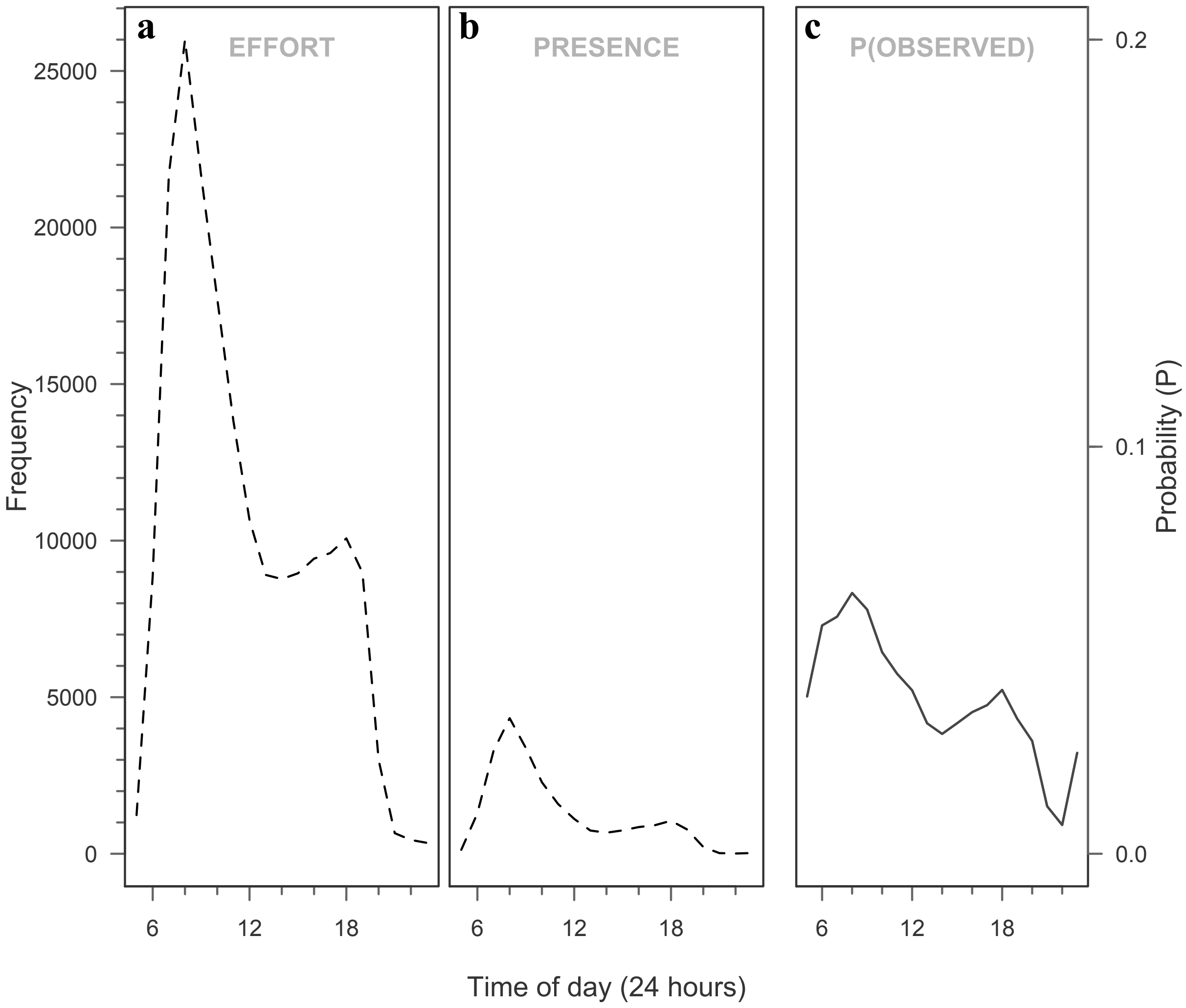

Figure S1: Example of methodology to normalise results – using all eBird data for Cooper's hawk (*Accipiter cooperii*) collected in the month of August. **a**) dashed line shows the binned frequency of all observations. **b**) dashed line shows the binned frequency of observations that sighted a Cooper's hawk. **c**) solid line shows the final probability of observing a Cooper's hawk (presence divided by effort).

MONTHLY PLOTS PER SPECIES

Species from North America (eBird data)

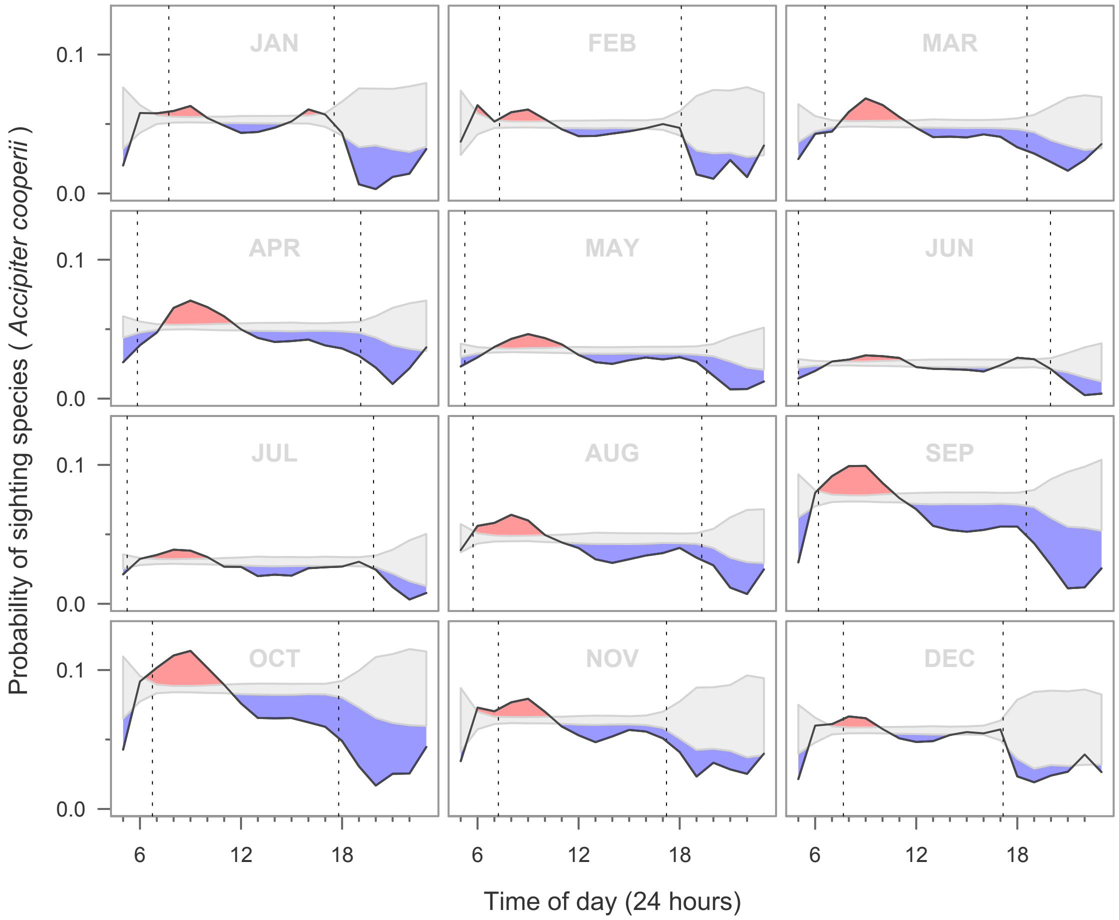

Figure S2: Probability of sighting predator (Cooper's hawk, *Accipiter cooperii*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

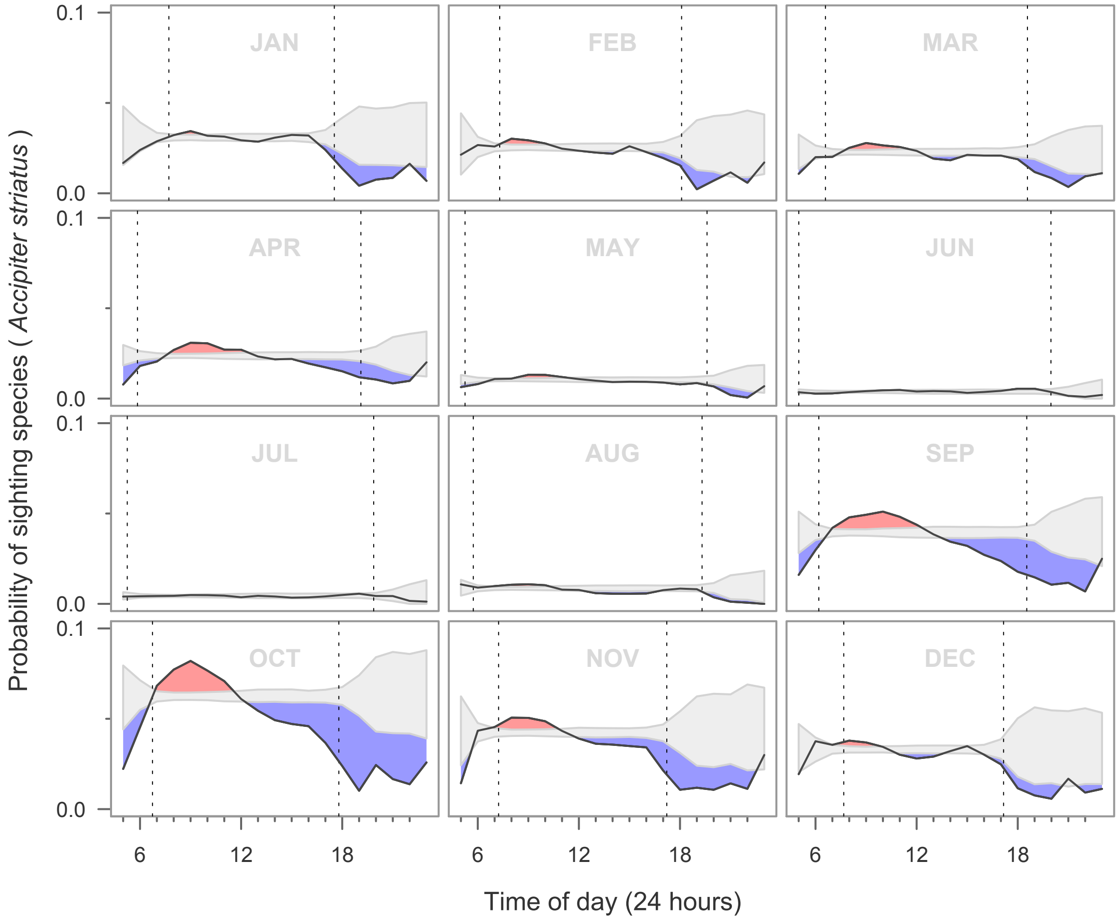

Figure S3: Probability of sighting predator (Sharp-shinned hawk, *Accipiter striatus*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

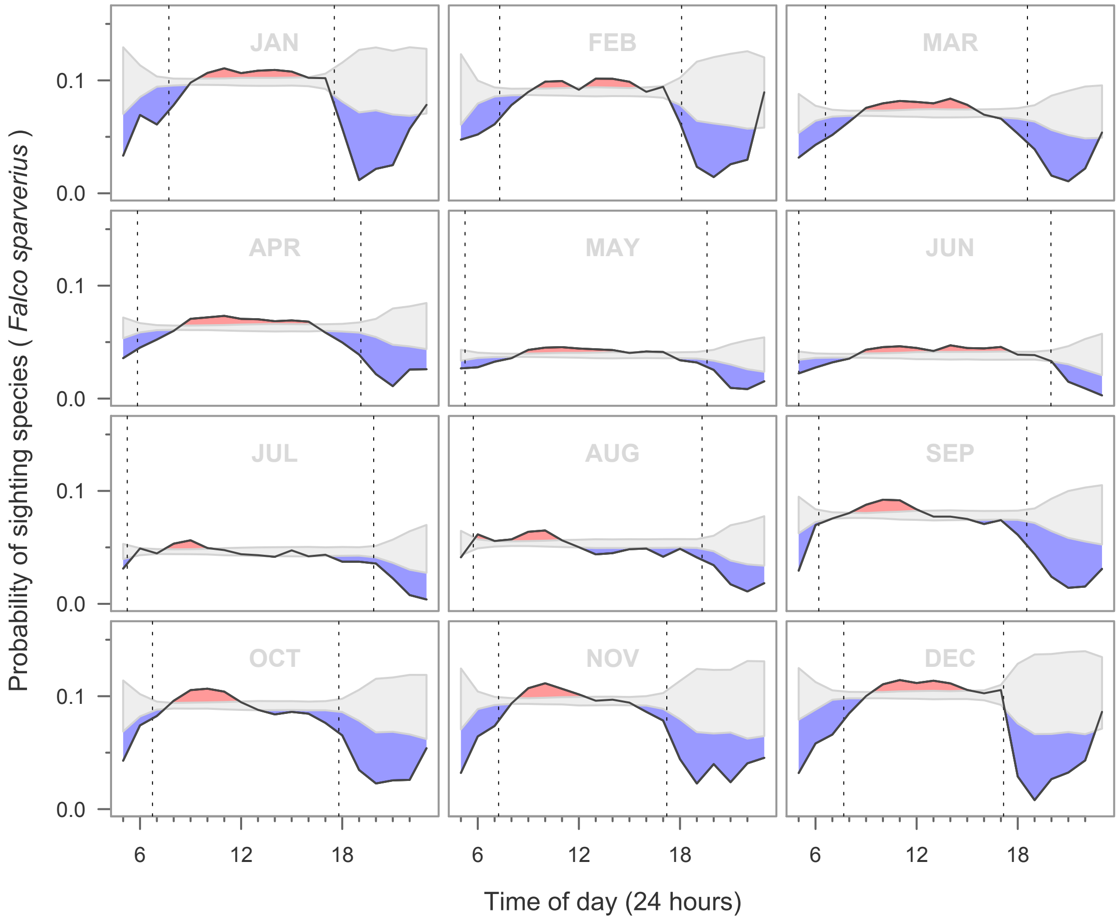

Figure S4: Probability of sighting predator (American kestrel, *Falco sparverius*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

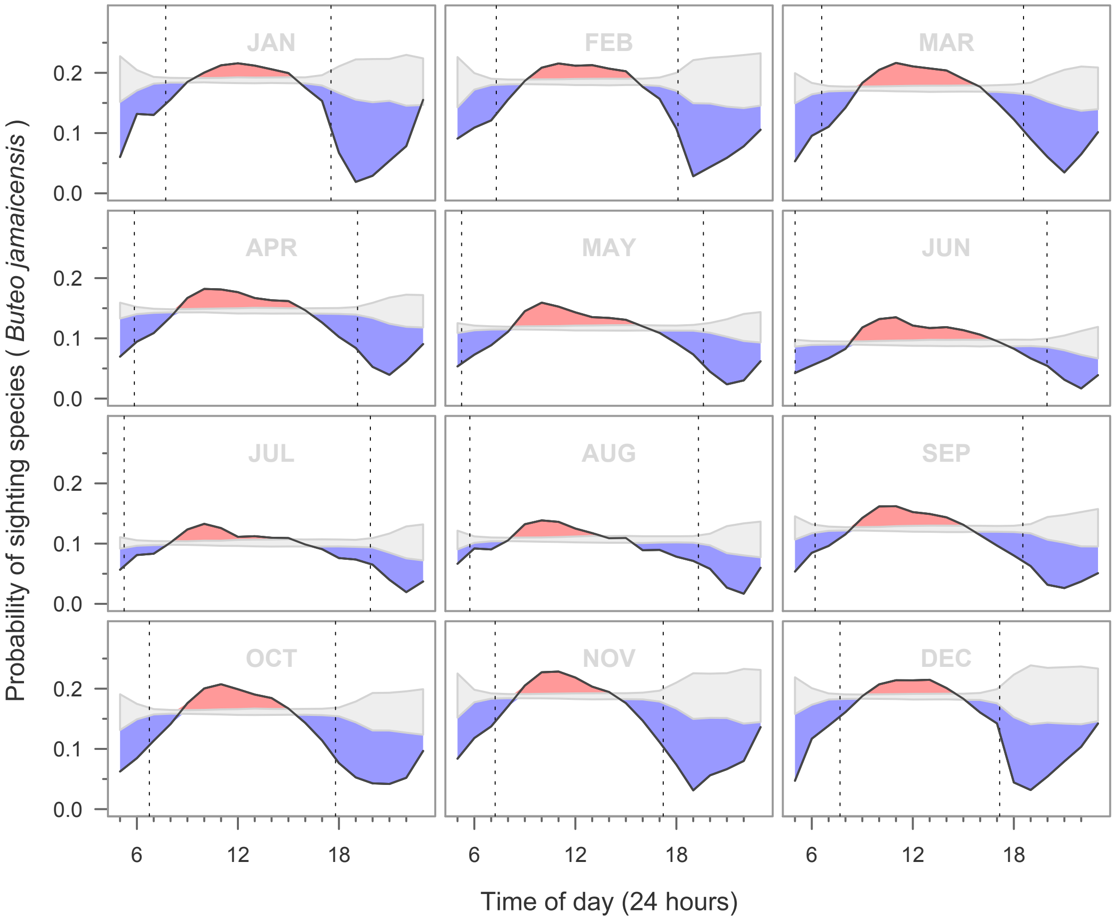

Figure S5: Probability of sighting predator (Red-tailed hawk, *Buteo jamaicensis*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

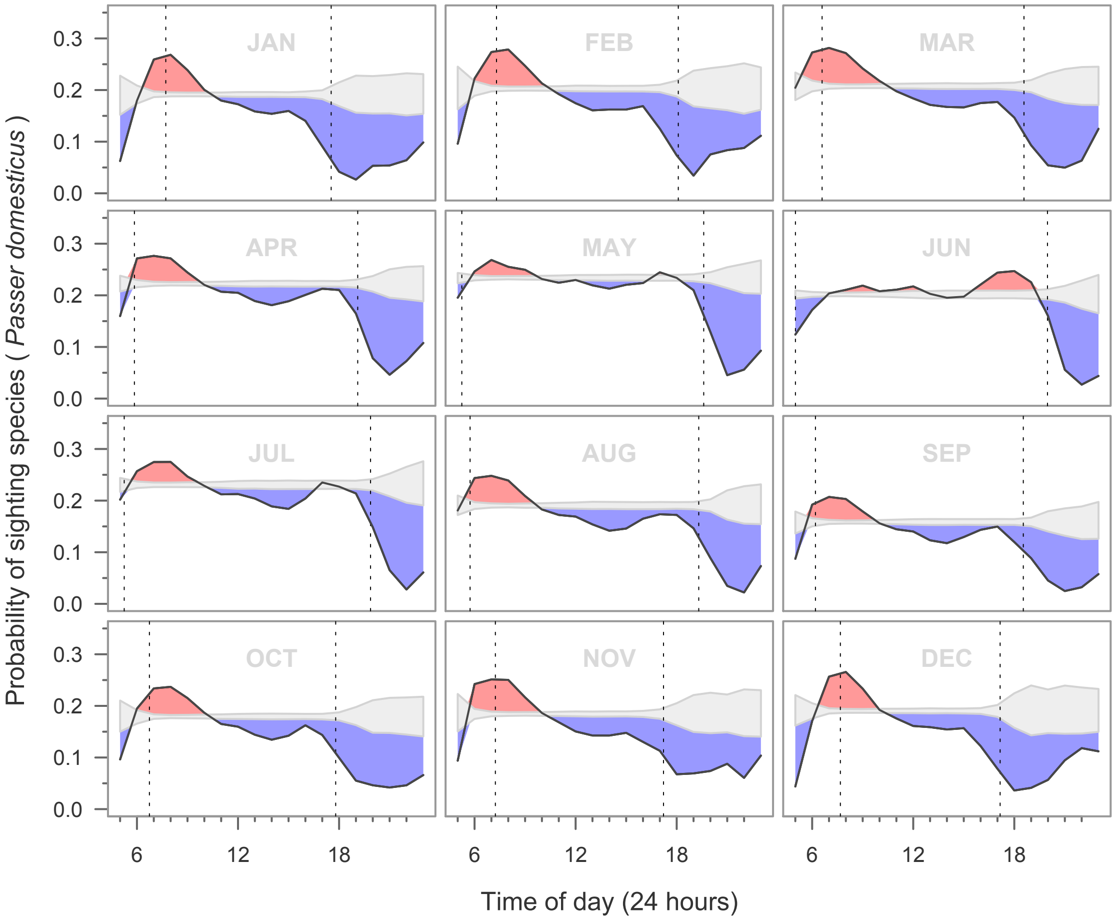

Figure S6: Probability of sighting prey (House sparrow, *Passer domesticus*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

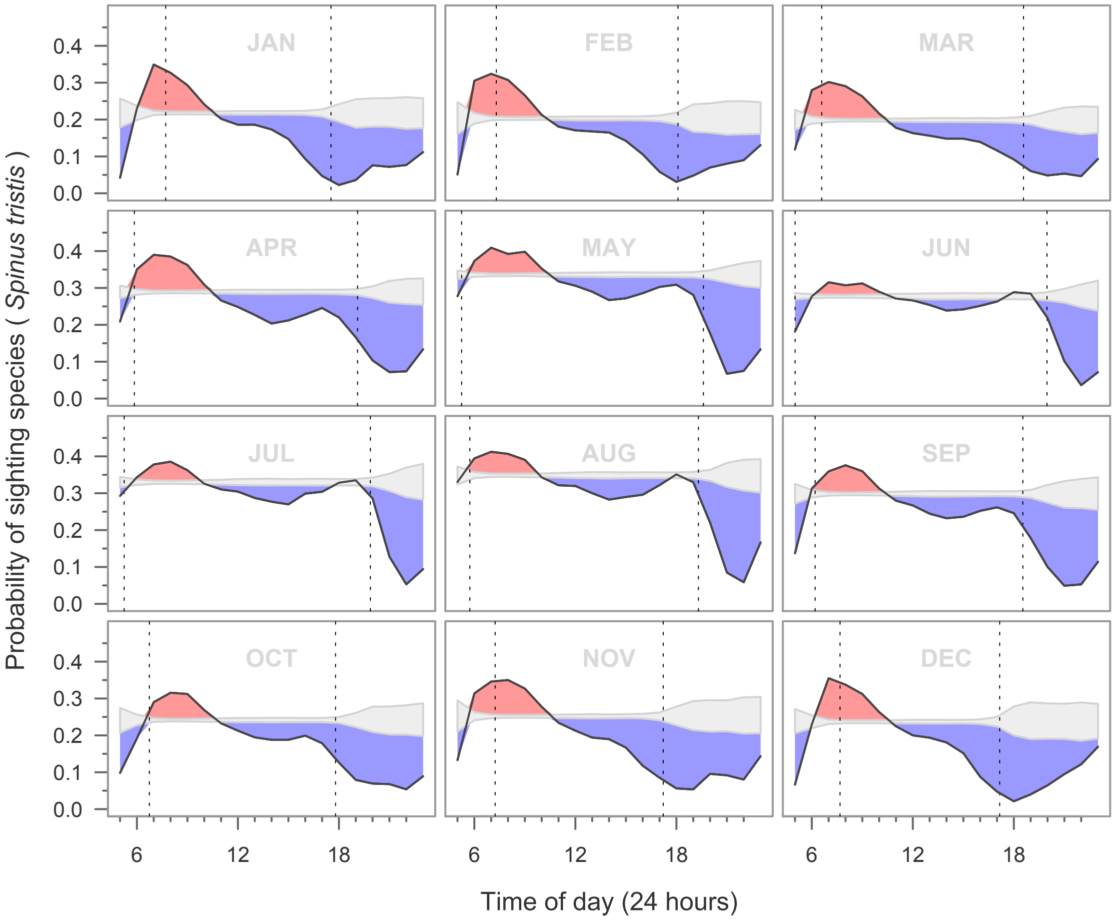

Figure S7: Probability of sighting prey (American goldfinch, *Spinus tristis*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

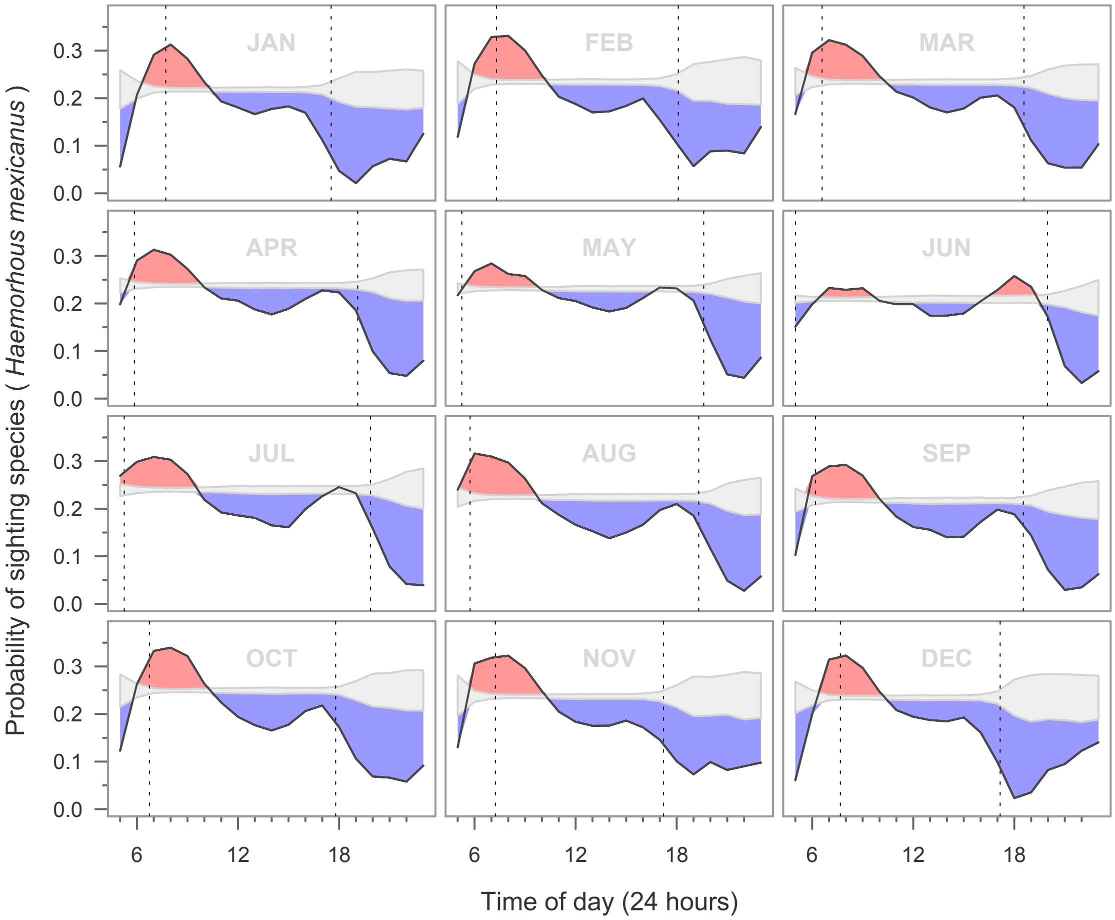

Figure S8: Probability of sighting prey (Housefinch, *Haemorhous mexicanus*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

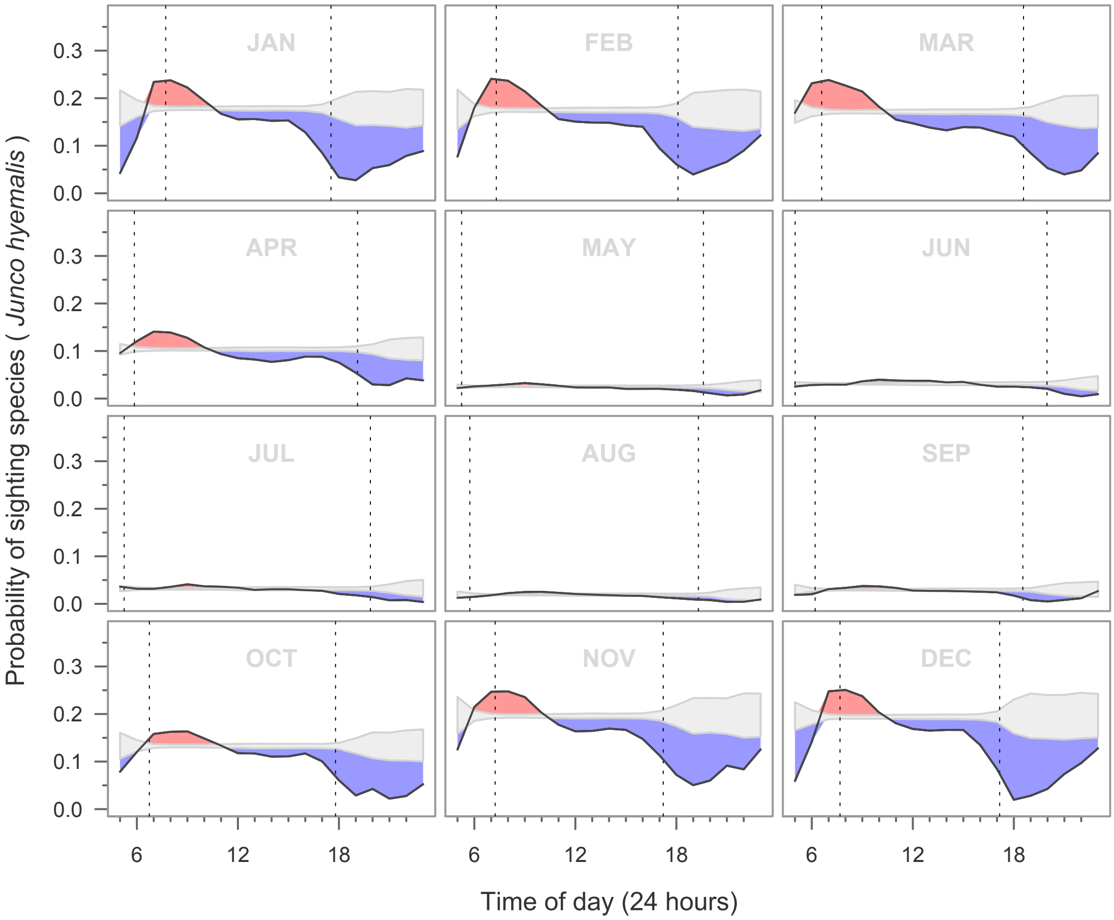

Figure S9: Probability of sighting prey (Dark-eyed junco, *Junco hyemalis*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

Species from Great Britain/Ireland (BirdTrack data)

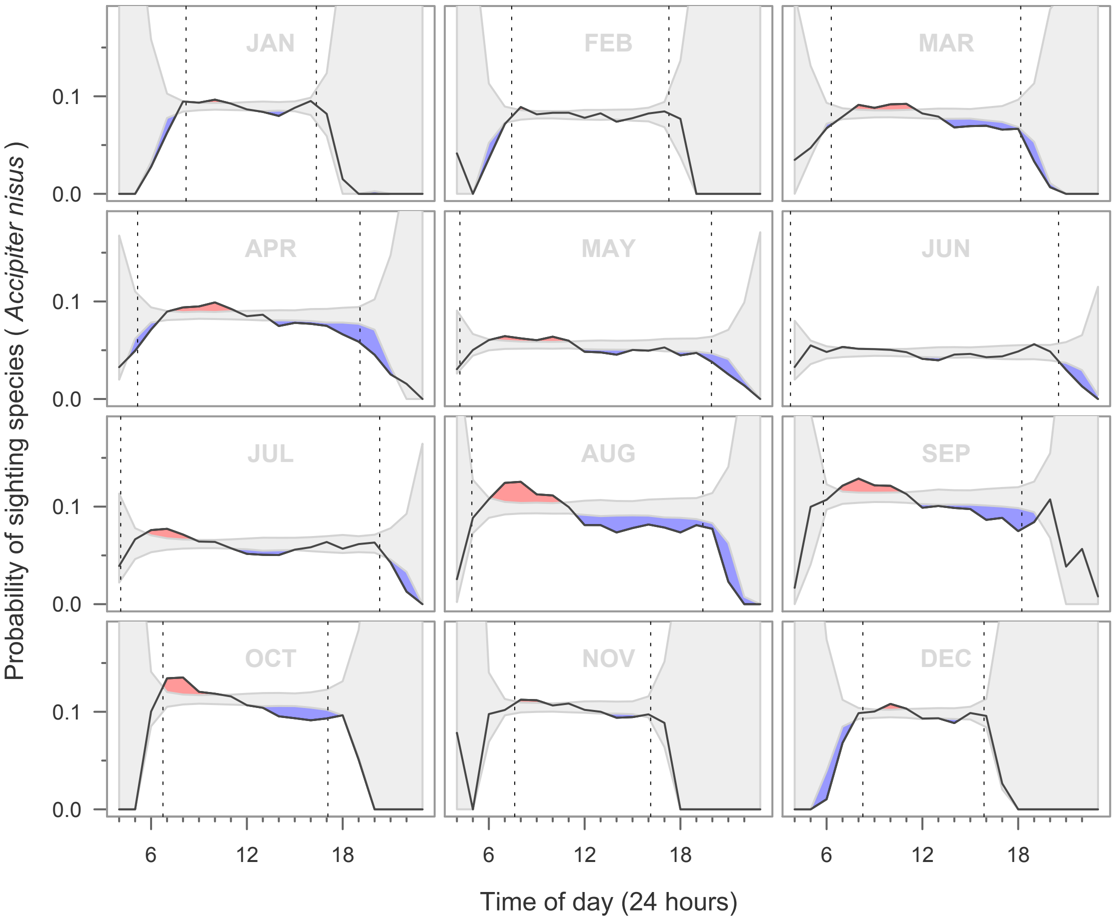

Figure S10: Probability of sighting predator (Sparrowhawk, *Accipiter nisus*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

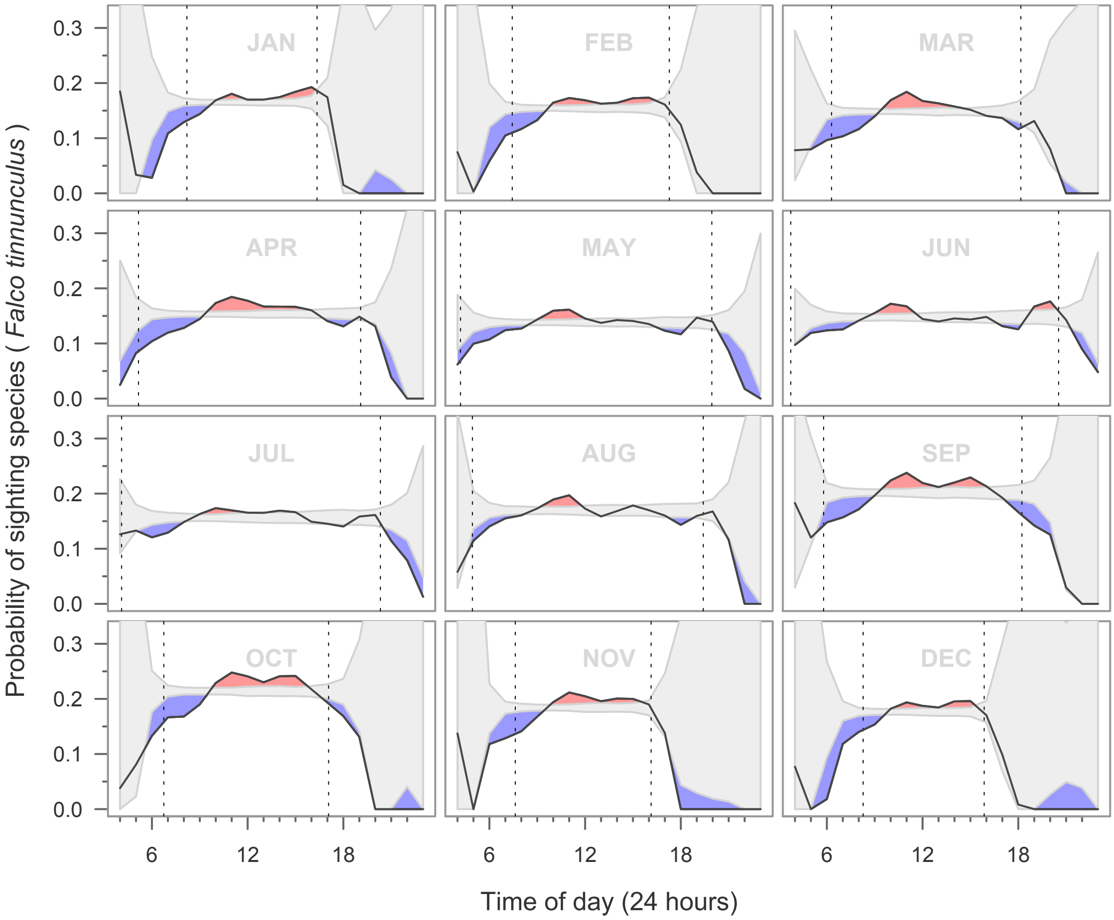

Figure S11: Probability of sighting predator (Kestrel, *Falco tinniculus*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

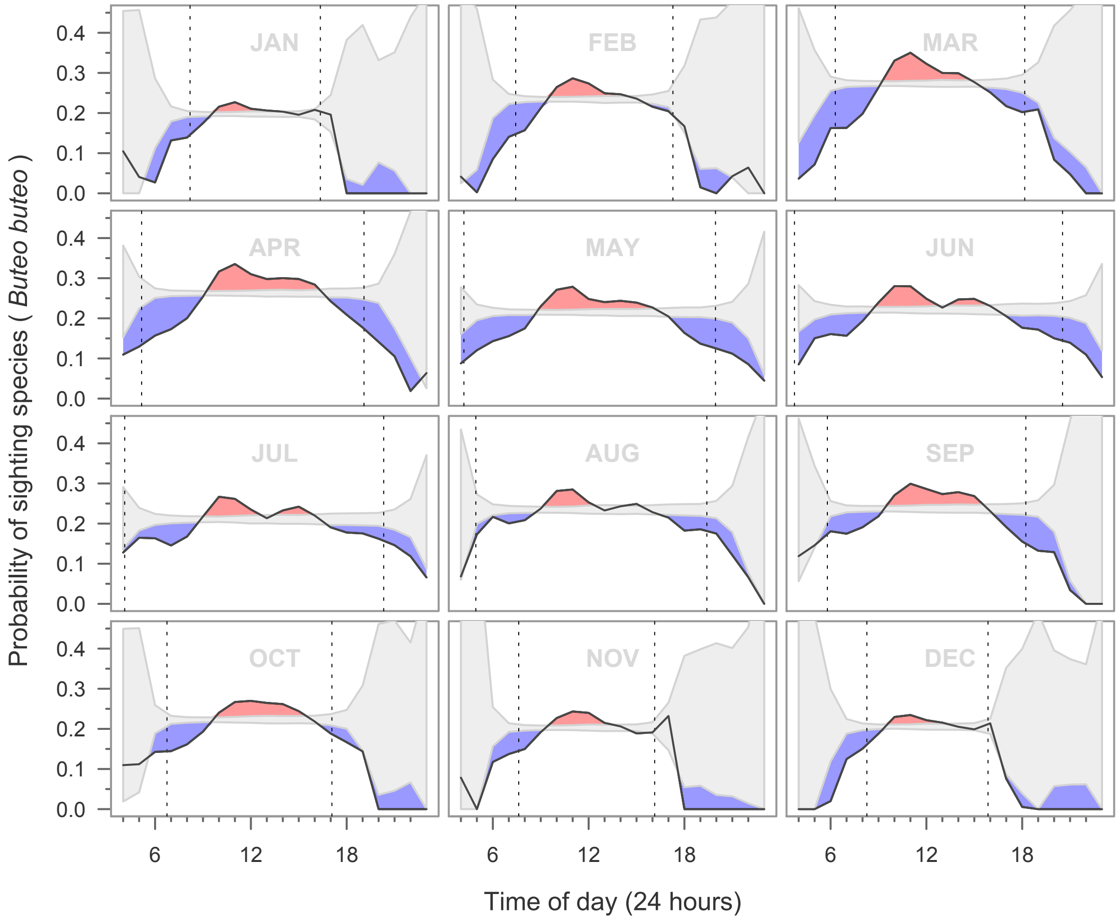

Figure S12: Probability of sighting predator (Buzzard, *Buteo buteo*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

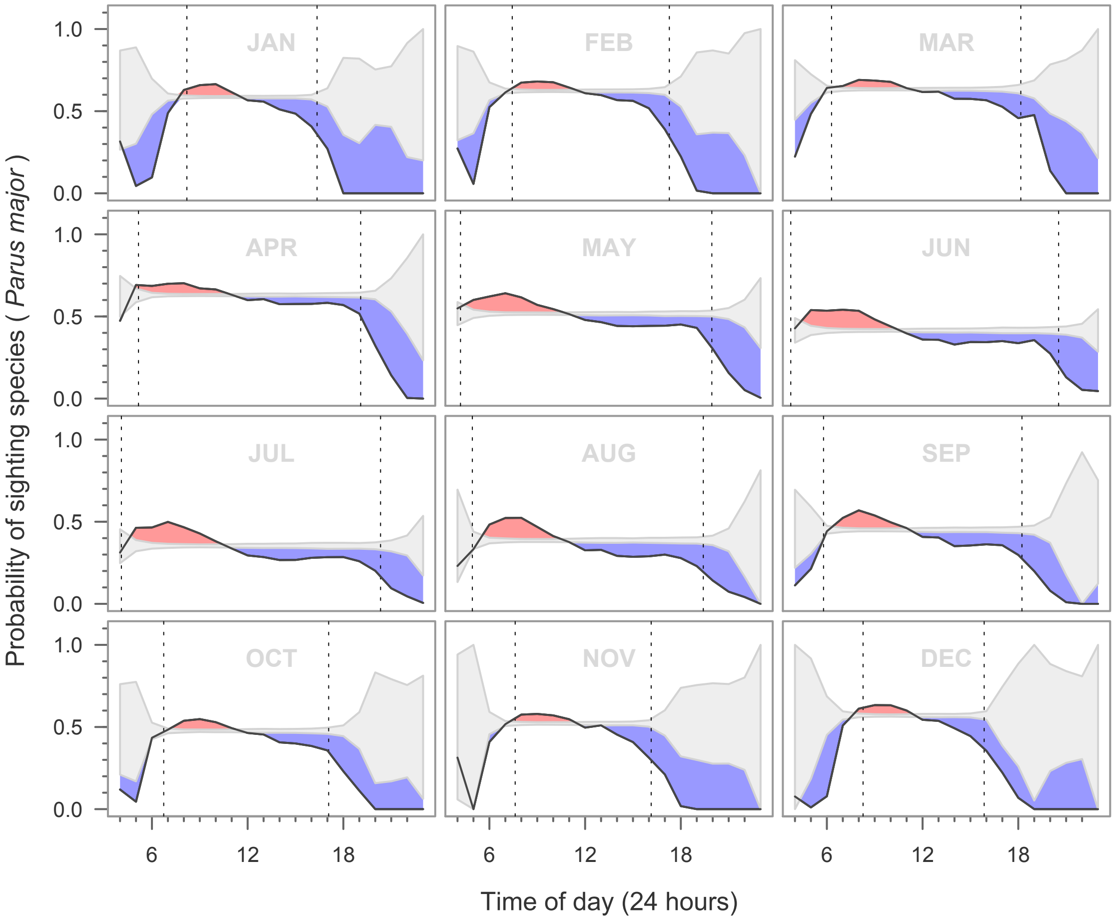

Figure S13: Probability of sighting prey (Great tit, *Parus major*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

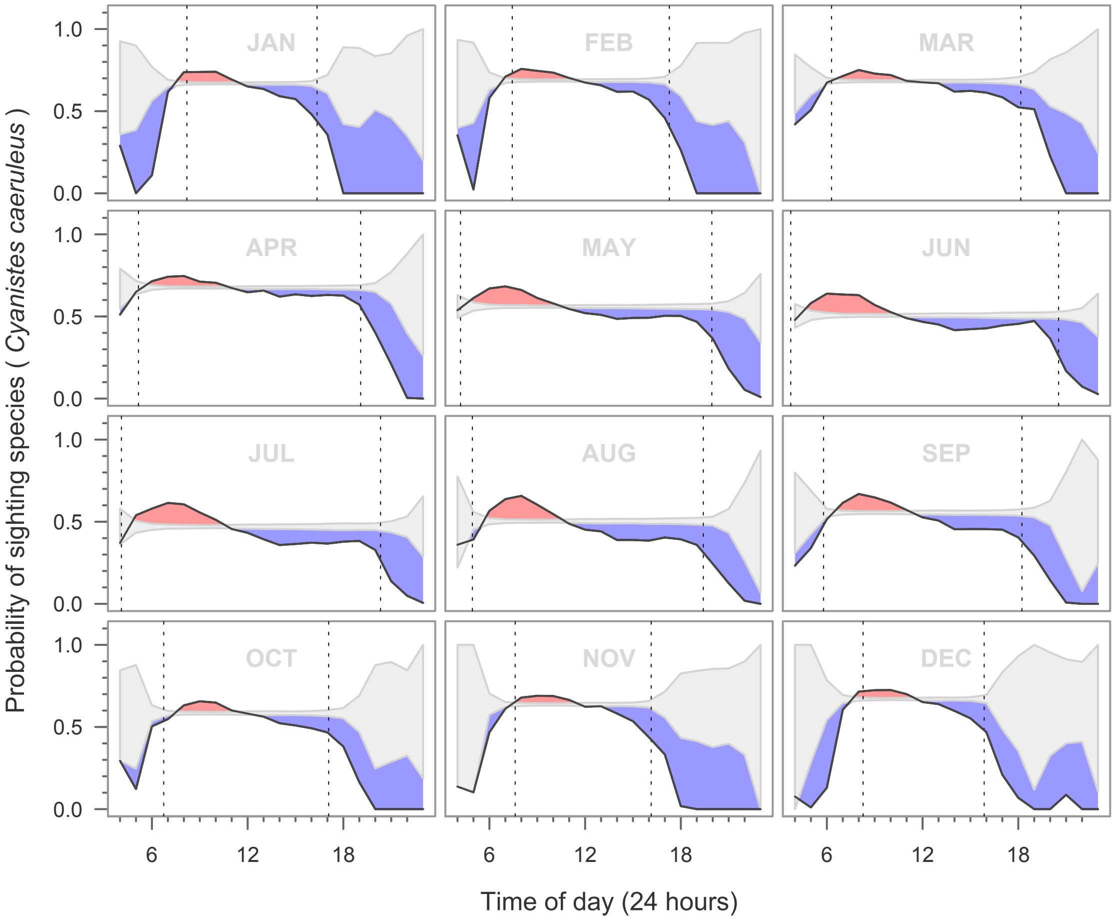

Figure S14: Probability of sighting prey (Blue tit, *Cyanistes caeruleus*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

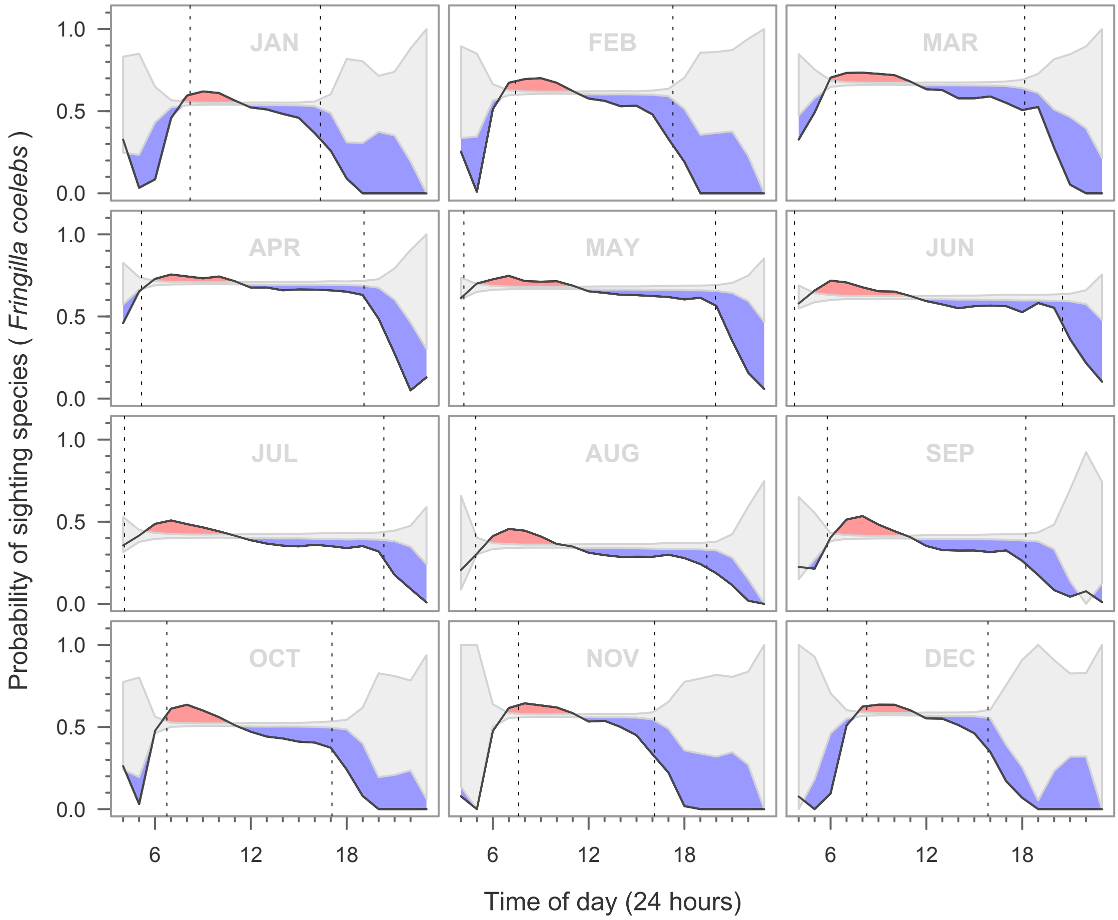

Figure S15: Probability of sighting prey (Chaffinch, *Fringilla coelebs*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

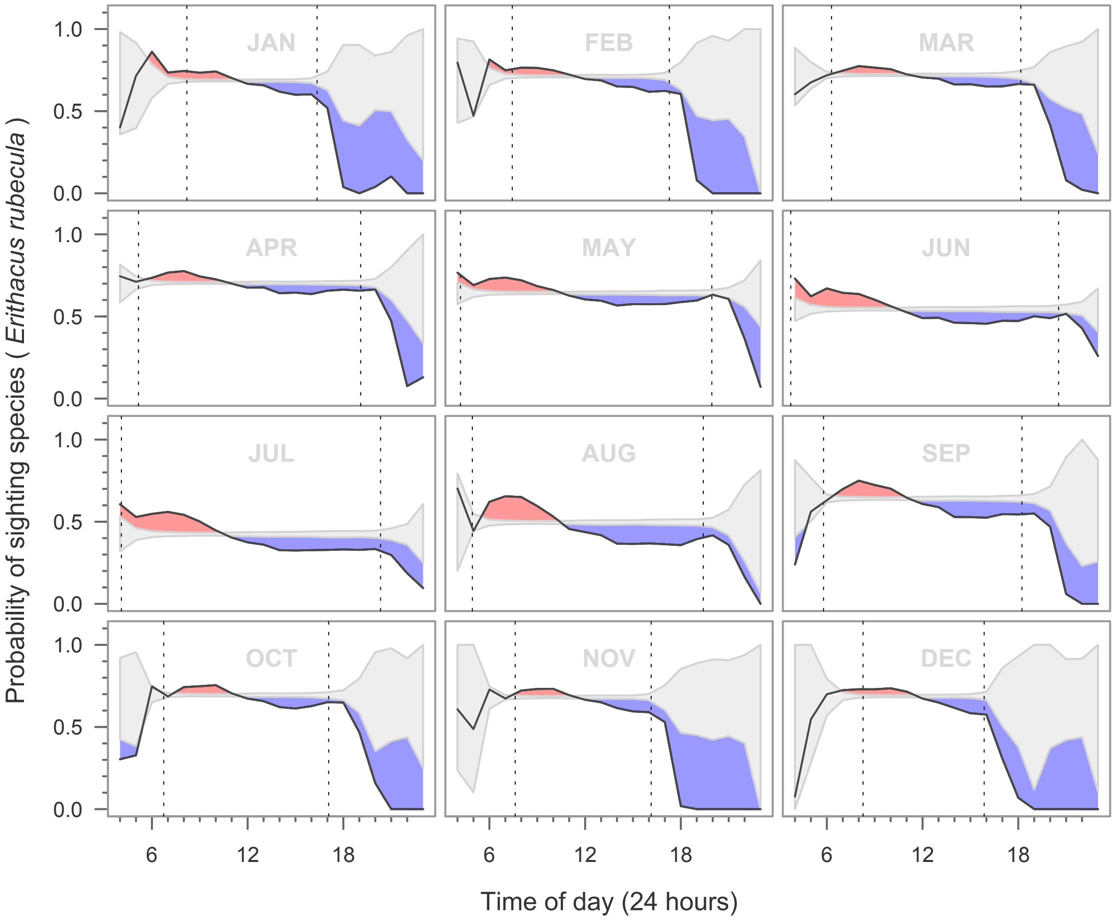

Figure S16: Probability of sighting prey (Robin, *Erithacus rubecula*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

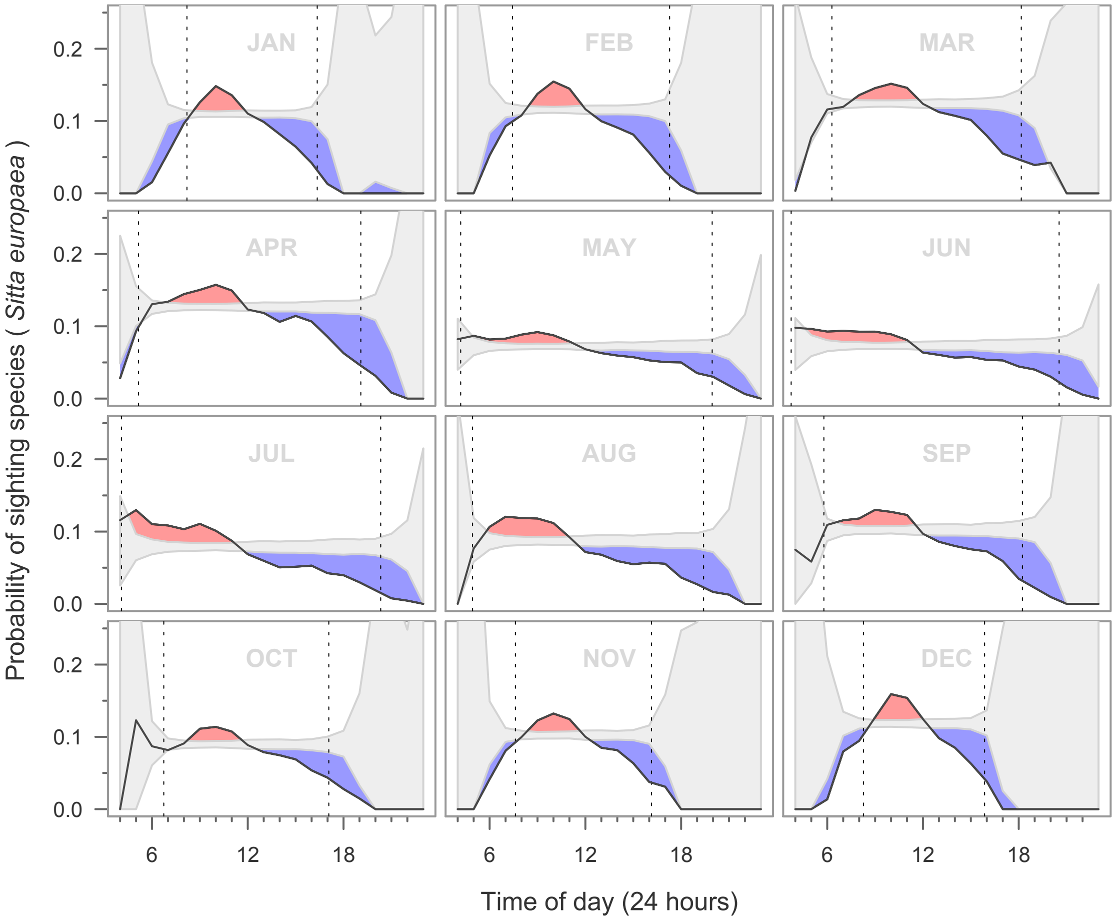

Figure S17: Probability of sighting prey (Nuthatch, *Sitta europaea*). Observed probability is shown by the black line, and the red polygon shows the 95% range of the distribution of 1000 randomised permutation tests on all observation data (presence and absence records). Dotted vertical lines denote average sunrise and sunset times from plotted data.

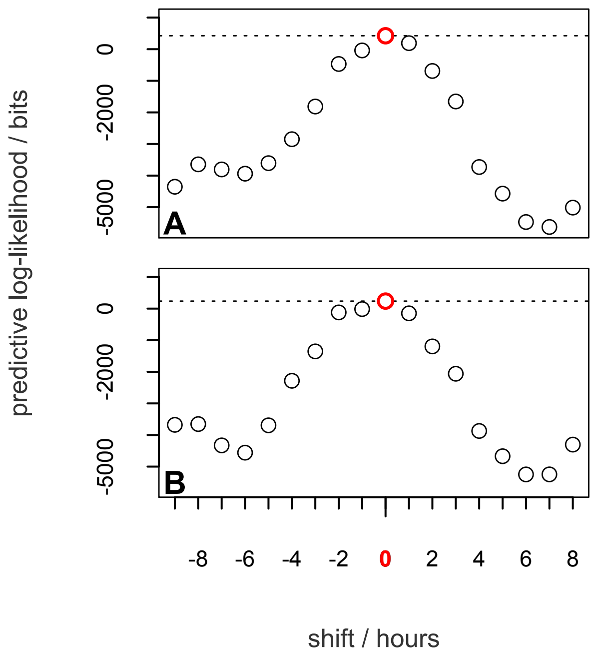

Figure S18: Predictive log-likelihood using shifted training data from 0 to 17 hours for species with predictive power greater than 0 (A) *P. domesticus*, and (B) *A. cooperii*. Due to the cyclical nature of the data pattern, 17 hours of forward shift is equal to 1 hour of backward shift, and thus to improve interpretation, 0 (marked in red) is mapped to the centre of the scale. The red points denote the predictive log-likelihood for zero shift (raw data), the level of which is shown across the figure by the horizontal dashed line. Comparing the profile of the predator (B) with the prey (A) species highlights the higher level of information when in negative predator time-shifted data (i.e. when the predator's data was shifted to be 1-2 hours earlier in the day) relative to the same amount of time shift of the prey species' data.

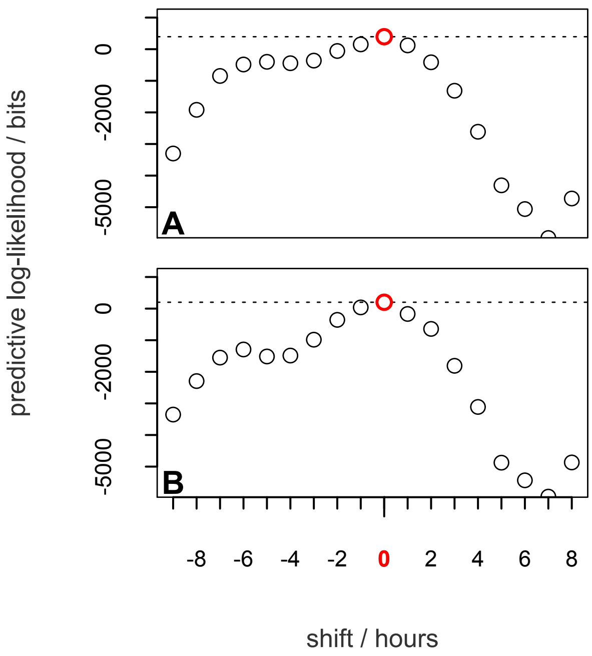

Figure S19: Predictive log-likelihood using shifted training data from 0 to 17 hours for species with predictive power greater than 0 (A) *F. coelebs* and (B) *A. nisus*. Due to the cyclical nature of the data pattern, 17 hours of forward shift is equal to 1 hour of backward shift, and thus to improve interpretation, 0 (marked in red) is mapped to the centre of the scale. The red points denote the predictive log-likelihood for zero shift (raw data), the level of which is shown across the figure by the horizontal dashed line. Comparing the profile of the predator (B) with the prey (A) species highlights the higher level of information when in negative predator time-shifted data (i.e. when the predator's data was shifted to approximately 1 hour earlier in the day) relative to the same amount of time shift of the prey species' data.