



Bird breeding season linked to sunshine hours in a marginally seasonal equatorial climate

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Abstract

The timing of reproduction is a fundamental aspect of life history, yet the breeding seasons of most birds of the world, i.e., those in the tropics, remain poorly understood. Here, we use more than 3000 mist-netting records and 300,000 citizen scientist observations collected over 6 years to characterize the nesting, incubation, fledging, and juvenile stages of the breeding season on Singapore Island in Southeast Asia's equatorial rainforest zone. The breeding season was compared with climate variables and food availability to identify possible proximate and ultimate causes. Breeding was seasonal and began just after the rainiest months of the year, when insect abundance was highest and when masting events were most likely to occur. While true photoperiod varied little throughout the year, overcast weather in November–December and sunnier weather in February–March caused average daily sunshine to increase by several hours at the onset of the breeding season in all 6 years. Our data suggest that subjective daily sunshine hours, which correlate with photoperiod at higher latitudes but not in the tropics, may be the actual proximate trigger of breeding activity in most of the world's birds.

Keywords Phenology · Breeding season · Ecology · Photoperiod · Tropics

Zusammenfassung

Die Vogel-Brutsaison in einem äquatorialen Klima mit geringfügiger Saisonalität ist an Sonnenstunden gekoppelt
Die zeitliche Koordinierung der Fortpflanzung ist ein grundlegender Aspekt des biologischen Lebenszyklus, und dennoch wissen wir immer noch sehr wenig über die Brutsaison der meisten Vögel der Welt, insbesondere der Vögel in den Tropen. In dieser Studie verwenden wir mehr als 3.000 Datenaufzeichnungen von Nebelnetz-Vogelfängen sowie 300.000 Beobachtungen von Bürgerforschungsplattformen – allesamt über einen Zeitraum von sechs Jahren gesammelt – um die Nist-, Inkubations-, Flüge- und Juvenil-Stadien der Brutzeit auf der Insel Singapur in der äquatorialen Regenwaldzone Südostasiens zu charakterisieren. Die Brutzeit wurde mit Klimavariablen und Daten bezüglich der Nahrungsverfügbarkeit verglichen, um mögliche proximate und ultimate Ursachen der zeitlichen Koordinierung zu identifizieren. Brutaktivität zeigte Saisonalität und begann kurz nach den regnerischsten Monaten des Jahres, wenn Insekten am häufigsten und Regenwald-Mastereignisse am wahrscheinlichsten waren. Obgleich die wahre Photoperiode das ganze Jahr über kaum variierte, führten bewölktes

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Wetter von November bis Dezember und sonnigeres Wetter von Februar bis März dazu, dass die durchschnittliche tägliche Sonneneinstrahlung zu Beginn der Brutzeit in allen sechs Jahren um mehrere Stunden zunahm. Unsere Daten deuten darauf hin, dass die subjektiven täglichen Sonnenstunden, die mit der Photoperiode zwar in höheren Breiten aber nicht in den Tropen korrelieren, bei den meisten Vögeln der Erde der eigentliche unmittelbare Auslöser der Brutaktivität sein könnten.

Introduction

Reproduction and reproductive cycles are central to the ecology and evolution of species, yet there is still no comprehensive understanding of what dictates reproductive seasonality in equatorial regions. The breeding seasonality of most temperate birds is known in immense detail based on centuries of field research by legions of ornithologists, both professional and amateur alike. In contrast, birds that breed in the tropics make up the vast majority of global avian diversity, but little is known about basic life-history aspects, including their breeding seasonality (Stutchbury and Morton 2001).

In temperate zones, reproduction typically takes place during the spring, when a gradually increasing daily photoperiod creates a seasonal rise in food availability (Van Der Jeugd et al. 2009; Visser et al. 2004). At lower latitudes, in semi-temperate savannah (Dittami 1987), subtropical montane forest (Auer et al. 2007), tropical savannah (Cox et al. 2013; Brandt and Creswell 2008), and tropical scrub (Diamond 1974) ecosystems, photoperiod varies less throughout the year and the more significant environmental variable is rainfall, with the breeding season often occurring in either the early wet season or the beginning of the dry season, depending on the site (Thomson 1950). Closest to the equator, in wet equatorial climates, rainfall is elevated throughout the year. Comparatively few studies have been conducted in these nearly aseasonal climates, and there is thought to be more variability between the timing of the breeding seasons of different species here (Auer et al. 2007; Steward et al. 2013; Stouffer et al. 2013). Breeding has been found to be aseasonal in some cases (Komdeur 1996; Tallman and Tallman 1997), but seasonal breeding is now generally accepted as the norm despite the limited climatic variation throughout the year (Baker 1939; Betts 1952; Catry et al. 2009; Chiver et al. 2015; Davos 1953; Fogden 1972; Gibson-Hill 1952; Ward 1969; Moreau 1950; Skutch 1950; Voous 1950; Snow and Snow 1964; Fogden 1972; Stiles 1980; Bell 1982; Tye 1992; McClure 1974; Morton 1971; Round 1982; Hau et al. 1998).

Here, we utilize more than 3000 mist-netting records and more than 300,000 citizen scientist observations collected over the course of more than 6 years in Singapore, a heavily urbanized tropical rainforest island near the equator. This type of multi-year banding data, which is necessary for seasonal studies, is rare in tropical regions. Citizen science records are an ever-expanding and underutilized resource which allows for a more comprehensive and multifaceted

analysis of seasonality when used in combination with more traditional data, and may have unexplored potential for sites where banding data are not available. In conducting this study, we had two objectives. Our first objective was to determine whether there is a distinct breeding season in Singapore and characterize the timing of four stages of that breeding season—nesting, incubation, fledging, and the emergence of independent juveniles. Seasonal timing of primary molt was also assessed. Our second goal was to identify the proximate and ultimate causes that dictate the timing of the breeding season at this site. The generally accepted paradigm is that the ultimate cause of seasonal breeding is food availability (Worthington 1982; Wunderle 1982; Young 1994; Zandt et al. 1990; Auer 2007, Cox et al. 2013; Ewald and Rohwer 1982; Fogden 1972; Grant and Boag 1980). Birds selectively breed at the time of year when food is most abundant and reproduction is most likely to be successful. To test the hypothesis that seasonality is linked to food availability, the seasonal reproductive patterns of different dietary guilds were compared. Some studies (Miller 1963) have cited migrant competition as a cause of breeding seasonality in the tropics, so seasonal migrant presence was also assessed as a variable. The proximate causes, or environmental triggers, for seasonality were also explored. The overwhelming majority of birds use photoperiod to regulate their phenological cycles (Cassone and Yoshimura 2015; Rowan 1926; Beebe et al. 2005). In tropical regions, where photoperiod varies little, some species are known to use climatic cues to regulate phenological cycles (Moore et al. 2005). It has also been suggested that improved body condition can act as a biological clock and trigger the onset of breeding (Medway and Wells 1976; Ward 1969). Sunshine hours, climatic variation, and body condition were all examined as potential proximate causes for the timing of the breeding season.

Methods

Study area

Singapore has a tropical everwet climate with only a small amount of seasonal variation. At latitude 1.3 N, photoperiod varies by only 9 min and average monthly temperature varies by only 2 °C over the course of the year (National Environmental Agency 2020). In contrast to monsoonal and savannah climates, there is no distinct wet or dry season.

Rainfall is elevated throughout the year, with higher rainfall occurring from November through January (Meteorological Service Singapore 2020). Unlike monsoonal and savannah climates, where fruiting and flowering typically occur during the rainy season, Southeast Asian equatorial sites like Singapore are dominated by dipterocarp and mixed dipterocarp forest in which fruiting and flowering occur continuously throughout the year, with supra-annual general flowering and mast fruiting events occurring irregularly every 1 to 9 years (Corlett 2019).

Data types

This study incorporates data from multiple sources. Six different reproductive and morphological variables were obtained from mist-netting records and from citizen science observations reported on www.eBird.org as of March 2019. Ten climatic variables were obtained from weather stations run by the National Environmental Agency of Singapore. All reproductive and morphological variables were either binomial or ordered discrete, while climatic variables were numeric.

Mist-netting records

Mist-netting sessions were conducted approximately once per month from 2013 to 2019. Standard morphological measurements, as well as age and the presence or absence of a brood patch, were collected from surveyed birds according to the EURING ringing system (EURING 2010). All netted birds were marked with permanent metal rings. Sampling effort was approximately 150 net-hours per month, using 5-shelf, 32 mm mesh size mist nets. A combination of 2.6 × 6 m, 2.6 × 9 m, and 2.6 × 12 m nets were used. This study includes the mist-netting records from the 53 most common resident land bird species (Online Resource 1). No shorebirds or migratory species were included. An average of 43 individuals were surveyed per month for a total of 3415 records. The majority (2102 captures) of the records are from Sungei Buloh Wetland Reserve, and the remaining (1313 captures) are from non-permanent netting locations in parks and nature reserves throughout the main island of Singapore (1.36 N, 103.81 E). Mist-netting records were used to determine seasonal brood patch presence, juvenile presence, pectoral muscle score, and molt.

Brood patch presence

The presence of a brood patch indicates that an individual is currently incubating eggs. Adult individuals were considered to have a brood patch if the breast was defeathered and the skin of the breast was either thick and vascularized, partially vascularized, or thin and wrinkled. Adults were

not considered to have a brood patch if the breast was feathered or in pin. According to the EURING ringing system, this corresponds to brood patch scores of 1–5 for the “present” category and a brood patch score of 0 for an “absent” brood patch (EURING 2010). Only adults were included when counting the proportion of the population with brood patches.

Juvenile presence

Individuals were considered to be juveniles if they retained a visible fleshy yellow gape and were still in their juvenile plumage, their first set of flight feathers. Juvenile plumage was identified from aligned growth bars in the remiges (Menzie 2015), a pattern of horizontal bands that appears when all feathers are grown simultaneously, the sharpness of the tips of primary feathers, and buffy brown edges on primary and secondary coverts. These stages correspond to the “3” and “3 J” age categories of the EURING ringing system (EURING 2010).

Pectoral muscle (PEC) score

PEC score is a measure of body condition. A higher PEC score indicates a better fed and more strongly muscled bird. PEC scores fall within 4 ordered categories (EURING 2010). A PEC score of 3 indicates robust pectoral muscles with a dimpled keel. A PEC score of 2 indicates healthy but less robust pectoral muscles that are even with the keel. A PEC score of 1 indicates an undernourished bird with thin pectoral muscles and a protruding keel. A PEC score of 0 indicates a bird near starvation with little-to-no pectoral muscle thickness.

Primary wing molt

Molt is the systematic process of feather loss and replacement which occurs once or twice per year in most species. Individuals were considered to be undergoing primary wing molt if one or more primary feathers were in pin or not fully emerged in symmetrical locations on both wings. Molt was structured as a binomial variable, where each individual either was (1) or was not (0) undergoing primary wing molt. A Chi-square test of independence was used to determine if there was any avoidance of breed-molt overlap, overlap being defined as individuals with both a brood patch and primary wing molt.

Citizen science records

Citizen science data were obtained from the March 2019 eBird basic dataset (eBird 2019). eBird is a public online platform for recording bird sightings and each observation

on eBird can optionally be accompanied by behavior codes, a subset of which are considered confirmed evidence of reproduction. These confirmed breeding codes were used to detect nesting behavior and the presence of fledglings. Records from Singapore from 2013 to 2019 of the same 53 common species included in the mist-netting dataset were utilized. The overall number of eBird observations has rapidly increased each year, because the number of site contributors has risen over time. Content on eBird is closely moderated and suspicious records are removed if they cannot be confirmed. Birds were considered to be nesting if they were observed carrying nesting material, building a nest, or occupying a nest (eBird codes CN, NB, and ON). Fledglings were considered to be present if recently fledged young were observed directly (eBird codes FY and FL). Nesting behavior and fledgling presence were structured as binomial variables. Each individual either did (1) or did not (0) exhibit nesting behavior and juveniles either were (1) or were not (0) present. Only some eBird contributors report breeding codes, so to avoid falsely inflated zeros, only records from observers who were actively reporting breeding codes within each respective year were included in the analysis. Records from observers who had not reported a breeding code within the calendar year were omitted. There were 234,881 observations recorded for Singapore between January 2013 and March 2019, of which 116,870 were of the 53 common species included in this study. Of those records, 61,395 were reported by observers who had recorded at least one breeding code in that calendar year, and of those 1343 included behavior codes. Each eBird checklist was only considered to have one data point per species, regardless of the number of individuals reported. For example, an observation of a group of two adults and one fledgling of the same species would be considered one observation of fledgling presence (one data point per checklist) rather than three observations (one data point per individual).

Presence of migratory passerines and near-passerines in Singapore was determined from observations on eBird. Migratory species from the orders Passeriformes, Caprimulgiformes, Coraciiformes, and Cuculiformes were included in the analysis for a total of 64 species (Online Resource 2). Species which are migratory in parts of their ranges but with resident populations in Singapore were omitted. Extremely rare vagrants which have been officially recorded in Singapore fewer than three times were also omitted. All of the migratory species included in this study arrive from northern Asia along the East Asian–Australasian flyway and are in Singapore only during their non-breeding period. Migrant presence was structured as a binomial variable, where each observed individual was either a migrant (1) or a resident (0). There were a total of 18,166 records of these 64 migrant species reported on eBird in Singapore between January 2013 and March 2019.

Climatic variables

Monthly records of ten climatic variables from 2013 to 2019 were utilized: number of rain days per month, maximum rainfall in a day (mm), total monthly rainfall (mm), mean relative humidity, mean daily sunshine hours (Watts/m²), mean daily temperature (°C), mean daily minimum temperature (°C), mean daily maximum temperature (°C), extreme maximum temperature (°C), and extreme minimum temperature (°C). Mean sunshine hours is the number of hours receiving direct irradiance of more than 120 Watts/m² and is influenced by both photoperiod and cloud cover. Data were recorded at the Changi Climate Station by the National Environmental Agency, Singapore, and is available under the Singapore Open Data License.

Data analysis

Two binomial generalized additive models were made for each binomial variable. Model 1 shows the full 6 year time series to best visualize annual periodicity. Model 2 is intended to give higher resolution on monthly variability and considers the full 6 year dataset as if it were a 1 year time series. Model 2 has a cyclical cubic regression spline, creating a trend line whose ends match in accordance with the cyclical annual pattern it is meant to model. Generalized additive models were generated using the *gam* function in R package *mgcv* (Wood 2011) and visualized using the R package *ggplot2* (Wickham 2016) and *lubridate* (Grolemund and Wickham 2011), which is robust to leap days and other quirks of time. The resulting trend lines can be interpreted as smoothed proportions of “positive values” (i.e., individuals with brood patches, nesting individuals, juvenile individuals) versus “negative values” (i.e., individuals without brood patches, non-nesting individuals, and adults) for a given date. Variables were structured binomially with modeled trend lines to maximize temporal resolution while minimizing small sample bias.

- Model 1: $\text{gam}(y \sim s(\text{date}), \text{binomial}, \text{data})$
- Model 2: $\text{gam}(y \sim s(\text{doy}, \text{bs} = \text{“cc”}), \text{binomial}, \text{data})$
- $y = \text{Binomial breeding variable (e.g., Nesting, Brood Patch)}$
- $\text{Date} = \text{full date (e.g., 11 June 2015)}$
- $\text{Doy} = \text{day of year (e.g., 11 June)}$.

The *ccf* function in R () was used to estimate the absolute maximum time-lagged cross-correlation for each pair of climatic variables and breeding variables. Breeding variables were averaged by month to allow for comparison with monthly climatic data. For each pair of variables, the cross-correlation was estimated for all potential lags (1-month lag,

2 month lag, etc.) and the absolute value of the strongest cross-correlation was reported.

Results

Seasonality

Breeding had a strong seasonal trend. All four stages of the reproductive cycle showed clear annual periodicity (Fig. 1; raw values without smoothing can be found in Online Resource 3). Nesting peaked between March and June of each year. The “nesting” variable includes observations of adults carrying nesting material, building nests, and sitting on nests, so the seasonal curve extends from the earliest stage of the breeding season up until just before the young fledge. The overall nesting trend has two peaks, one in March and a second one in June. The secondary peak in June can mostly be attributed to observations of the granivorous Baya Weaver, which nests later in the season than birds of other dietary guilds.

Brood patch presence peaked in April–May of each year (Fig. 1b). Fledgling presence peaked in June–July of the final 3 years of the study, from 2016 onwards, and there were seasonal peaks in all years except 2014. In the first 3 years of the study, sample size in citizen science data was very low. In 2013–2015 there were only 23 fledgling records, while

in 2016–2018, there were 427. Given that 2014 has peaks in nesting, brood patch, and juvenile presence at the usual times, the absence of a peak in fledgling presence is best attributed to low sample size: there were only two records of fledglings in 2014. The presence of independent juveniles peaked in August–September in all 6 years of the study.

Molt

Molt did not exhibit a clear annual trend (Fig. 2a). Evidence of a post-nuptial molt in August was seen in 4 out of 6 years, and peaks in January 2014 and January 2017 indicate pre-nuptial molts in those years, but other years exhibited contradictory patterns. In 2016, very few individuals were molting at the ‘typical’ times during January and August, and instead, there was a peak in May, during the breeding season. Yet, despite the atypical timing of the 2016 molt, there was no increase in brood-molt overlap during that year (Fig. 2, dotplot). That is to say, although there was a large proportion of individuals undergoing primary wing molt in May, the month when brood patch presence is at its peak, there was no increase in the number of individuals simultaneously molting and incubating eggs as compared to any other year. There was no avoidance of brood-molt overlap. Individuals were equally likely to be molting primary feathers regardless of whether or not they were incubating eggs ($\chi^2(1, N=2900)=0.08, p=0.77$, Online Resource 4).

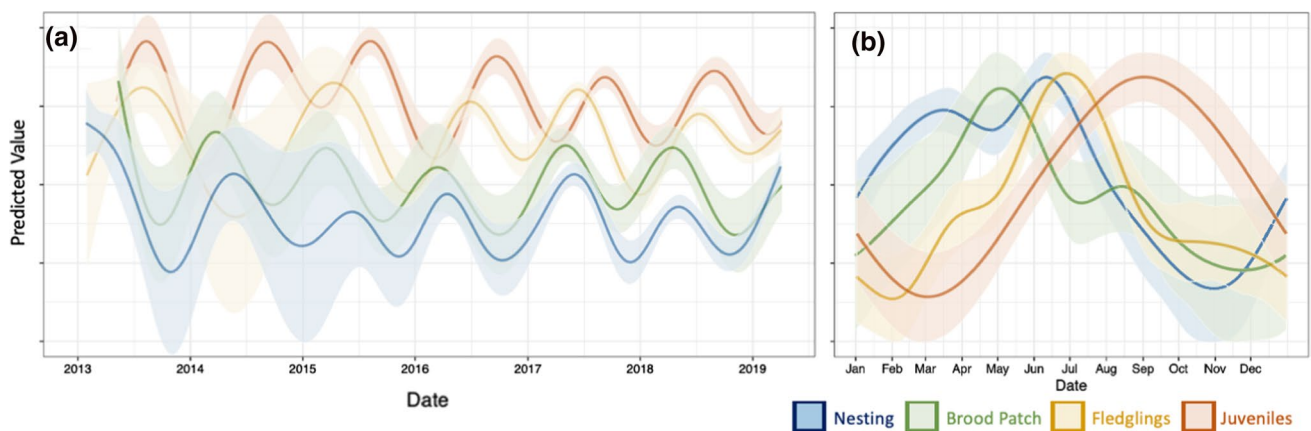


Fig. 1 Binomial generalized additive models structured by **a** full calendar date and **b** day of year, of nesting activity (eBird codes CN, NB, ON, $k=18$), fledgling presence (eBird codes FL, FY, $k=13$), brood patch presence ($k=15$), and juvenile presence ($k=15$), in Singapore; k values indicate the maximum number of basis functions used to generate smooth terms in each generalized additive model. Nesting and fledgling data were from the March 2019 eBird basic dataset for Singapore, including only records from observers who had reported at least one breeding code within each respective calendar year. Brood patch and juvenile data were from mist-netting records of resident land birds in Singapore. Data include 217 nesting observations and 273 fledgling observations out of 61,395 total eBird obser-

ations, as well as 373 juveniles and 352 adults with brood patches among 1465 mist-netted birds from 53 species of resident land birds. Observations range from 1 January 2013 until 31 March 2019. Brood patch absence considers only adult individuals. Year labels are placed on the first day of each year. Month labels are placed on the first day of each month. Predicted values of each of the four variables come from separate models and are not directly comparable, so they have been staggered along the Y-axis for better visibility. Y-axis values can be interpreted as the proportion of individuals observed with positive values of a breeding variable (i.e., nesting, with brood patches) versus negative values (i.e., not nesting, without brood patches) at a given time

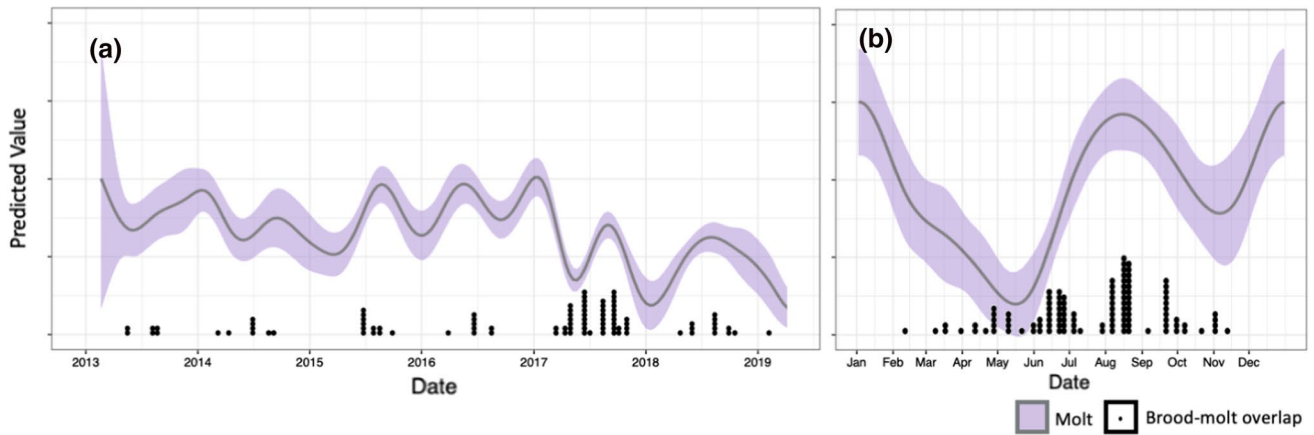


Fig. 2 Binomial generalized additive models structured by **a** full calendar date and **b** day of year of primary wing molt. Data are from mist-netting records of 53 species of resident land birds in Singapore, including 988 individuals molting flight feathers and 1046 not molting among a total of 2034 surveyed birds. Dotplot indicates individu-

als simultaneously brooding eggs (with brood patches) and undergoing primary wing molt. Observations range from 21 February 2013 until 31 March 2019. Year labels are placed on the first day of each year. Month labels are placed on the first day of each month

Dietary guilds

Frugivores and insectivores (see Online Resource 1) shared the same breeding season. Members of both guilds were found to nest in February–June, fledge in June–July, and have independent juveniles in September (Fig. 3a–b). Sample size was highest for insectivores, lower for frugivores, and lowest for granivores. There is little grassland habitat in Singapore and only a few granivorous species,

so there are comparatively little data on granivores. This dataset includes records of only three granivorous species: Baya Weavers, Javan Munias, and Scaly-breasted Munias, with Baya Weavers making up the vast majority. Granivores may have a distinct breeding season, but data are lacking. The nesting season of granivores occurs primarily in June, starting later but still falling within the longer nesting season of frugivores and insectivores (Fig. 3c).

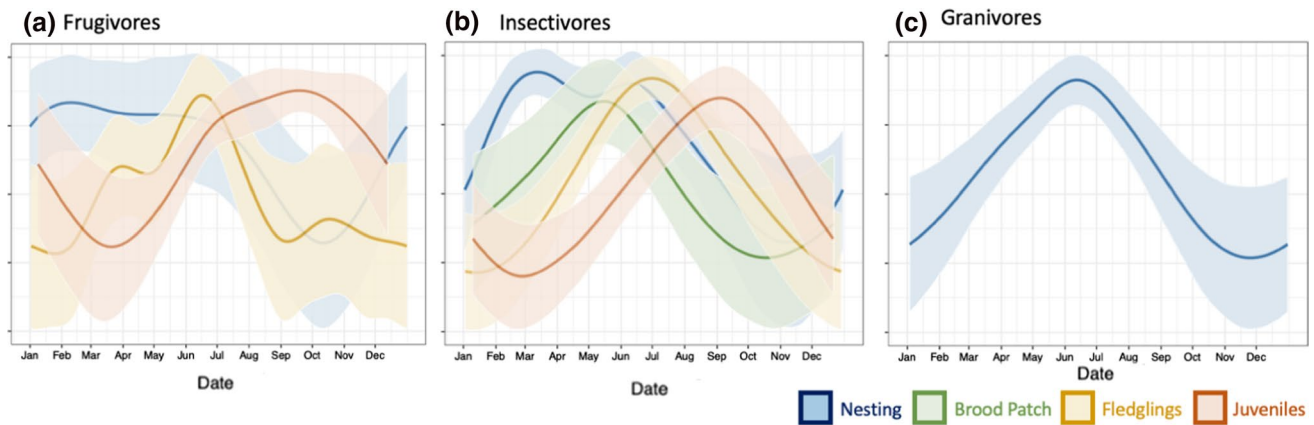


Fig. 3 Binomial cyclic basis spline generalized additive models of nesting activity (eBird codes CN, NB, ON), fledgling presence (eBird codes FL, FY), brood patch presence, and juvenile presence among three dietary guilds of resident land birds in Singapore. Species not corresponding to one of these three dietary guilds were omitted. Data are from the March 2019 eBird basic dataset for Singapore, including only records from observers who had reported at least one breeding code within each respective calendar year, and from mist-netting records. Data include records from 1 January 2013 until 31 March 2019. Some trend lines are omitted from the frugivore and granivore

dietary guilds, because there were not enough observations of brood patches among frugivores, or brood patches, fledglings, and juveniles among granivores to characterize statistically significant seasonal trends. Month labels are placed on the first day of each month. **a** Frugivores: 40 nests and 29 fledglings out of 12,431 total citizen science observations, 76 juveniles out of 220 total mist-netted birds. **b** Insectivores: 50 nests and 66 fledglings out of 15,701 total citizen science observations; 205 adults with brood patches and 144 juveniles out of 849 total mist-netted birds. **c** Granivores: 44 nests out of 1256 total observations

Migrants

Migrant presence had a strong seasonal pattern (Fig. 4). A large number of migrants are seen from November through March. In November, the month of highest abundance, migrants make up a quarter of all observed birds in Singapore. Few to none are seen in June–August. The seasonal minima in migrant presence occur at approximately the same time as the peaks in fledgling presence each year. There was a strong time-lagged cross-correlation between migrant and brood patch presence ($r=0.75$) and migrant and juvenile presence ($r=0.82$).

Body condition

Body condition exhibited an annual cyclic pattern that corresponded with the breeding season (Fig. 5). In all 6 years, average PEC score decreased over the course of the breeding season in April–July, and rallied over the course of the

non-breeding months August–December. Individuals in excellent body condition, with a PEC score of 3, were most common in January–April, but could be found during all months of the year. PEC scores of 2, indicating average body condition, were by far the most common (Fig. 6).

Climate

According to monthly weather data from the Changi Climate Station collected from 2013–2019, in most years, October–December are the rainiest months, with higher humidity and fewer sunshine hours (Fig. 7c–e). February is usually the driest month and tends to have the most daily sunshine hours. Although true photoperiod only varies by 9 min throughout the year, sunshine hours can vary by as much as 5 h due to changes in cloud cover (Fig. 7a–b). A monthly average of more than 8 h of sunshine per day was only ever reported in February and March, and fewer than 4 h per day were only ever reported in November and

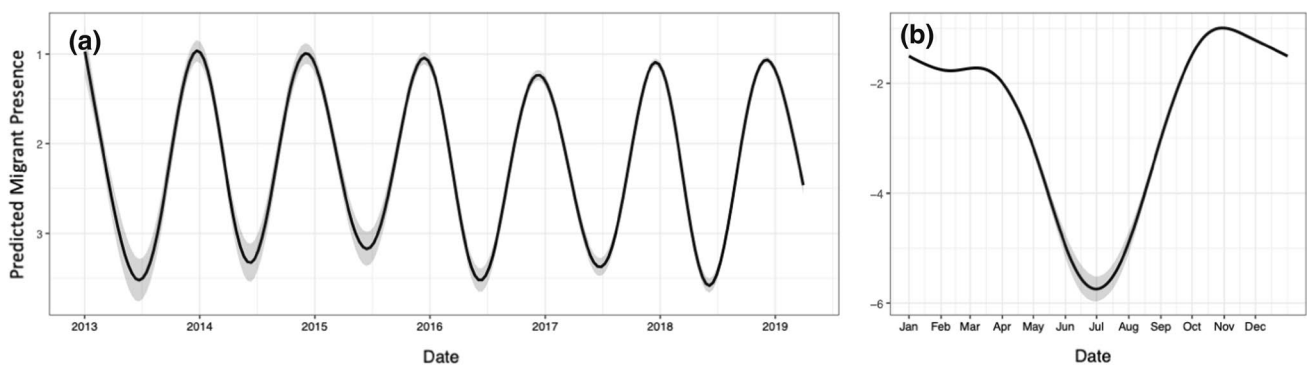


Fig. 4 Binomial generalized additive models structured by **a** full calendar date and **b** day of year of migrant presence. Data are from March 2019 eBird basic dataset for Singapore. Data include records from 1 January 2013 until 31 March 2019. Year labels are placed on

the first day of each year. Month labels are placed on the first day of each month. Data include 18,166 migrants and 116,870 residents for a total of 135,036 observations

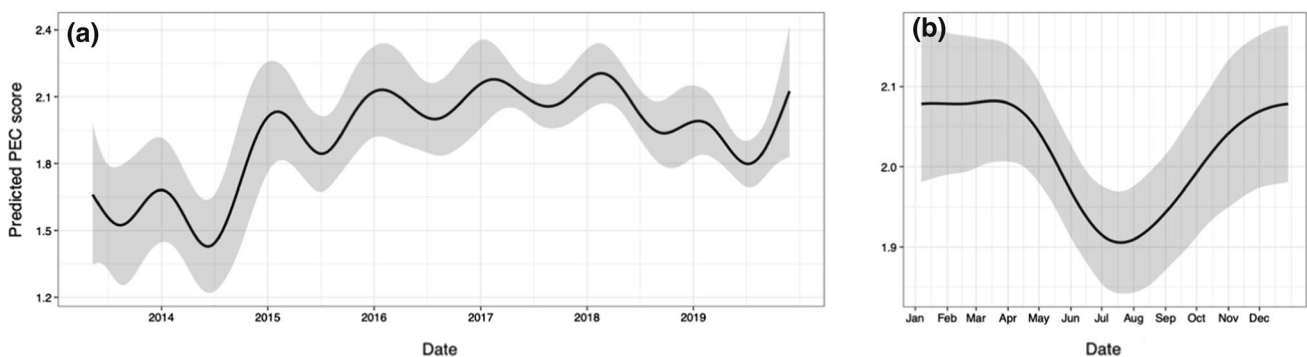


Fig. 5 Binomial generalized additive models structured by **a** full calendar date and **b** day of year of pectoral muscle score (PEC). Data include mist-netting records from 1103 adult individuals from 53 species of resident land birds in Singapore. Observations range from 21

February 2013 until 31 March 2019. Year labels are placed on the first day of each year. Month labels are placed on the first day of each month

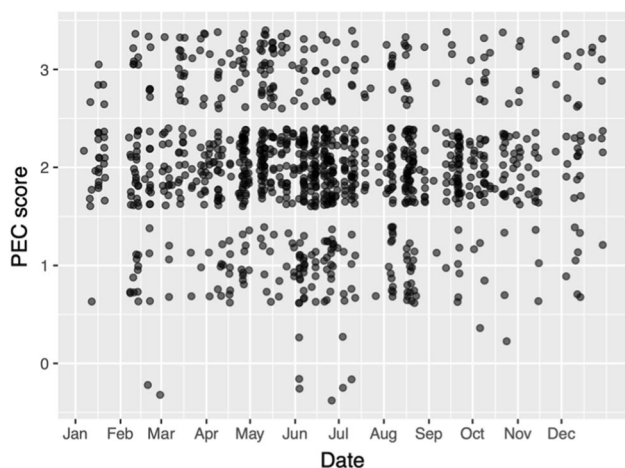


Fig. 6 Pectoral muscle (PEC) scores, indicating body condition of 1103 adult individuals from 53 resident species of land birds in Singapore collected from 21 February 2013 to 31 March. Jitter was added to the display of PEC scores (0, 1, 2, and 3) to mask overlap. Sample sizes for each discrete PEC score are 3:193, 2:722, 1:177, and 0:11

December, the wettest months. In all 6 years mean daily sunshine increased by 3.5–5.5 h from November to February (red lines, Fig. 7a–b). Positive trends in sunshine hours during other times of year never lasted more than 2 months and never exceeded a 3.5 h increase. Mean relative humidity followed a trend similar to rainfall, but was less regular between years. Mean temperature was 1–2° C higher during the middle of the year, with peak temperatures usually occurring in April (Fig. 7f–k). Among pairwise comparisons of breeding and climatic variables, the strongest cross-correlations were mean daily minimum temperature \times juvenile presence ($r=0.71$) and mean temperature \times juvenile presence ($r=0.68$, Online Resource 5), but the magnitude of the seasonal variation in these climatic variables was small at only 1–2° C (Fig. 7f–j).

Discussion

Singapore's avifauna breeds in a seasonal fashion

Resident birds in Singapore breed seasonally (Fig. 1), in agreement with studies from multiple other tropical and subtropical rainforest sites across the planet (Table 1), including in Panama (Wikelski et al. 2000), Argentina (Auer et al. 2007), Thailand (McClure 1974), and Sarawak (Fogden 1972). Although climatic seasonality in Singapore is limited, with a high noise-to-signal ratio, there are distinguishable patterns in sunshine hours and rainfall with which the breeding season seems to align. Sites with aseasonal breeding (lowland Cameroon and eastern Ecuador;

Table 1) appear to occur primarily in the transition zone between the wet-summer rainfall pattern seen north of the equator and the wet-winter rainfall pattern seen south of the equator (green and magenta colors, Fig. 8). In Southeast Asia, this climatic transition zone is found about 1000 km north of Singapore, at the isthmus of Kra on the Thai-Malay peninsula.

The timing of the breeding season in Singapore matches the seasonality seen in other parts of equatorial Southeast Asia. Sarawak, Borneo, has a rainfall pattern similar to Singapore, with peak rainfall occurring in December and January, and the breeding season occurs at a similar time. In Sarawak brood patches are seen from January until June, with a peak in March (Fogden 1972), which is slightly earlier than Singapore. Seasonality of insect abundance is also similar between the two sites, being highest during the first half of the year and increasing only a few fold (Fogden 1970). Khao Yai, Thailand, also shares a similar breeding season. Birds nest during the hotter, drier months, which are also the months of highest insect abundance. Nests are found in Khao Yai from January until May (McClure 1974), a seasonal pattern similar to the one seen in Singapore.

Molt in Singapore is not seasonal

Although breeding was seasonal in our dataset, molt was not (Fig. 2). Indeed, there was no evidence that Singaporean birds avoid breed-molt overlap (Online Resource 4). Birds generally tend to avoid breeding and molting simultaneously (Craig 1983; Payne 1969; Ralph, Fancy 1994; Snow and Snow 1964; Snow 1976). Where this occurs, breed-molt overlap is more common among tropical birds than temperate ones (Foster 1975; Johnson et al. 2012), and especially common among aseasonally breeding birds (Dittami 1987; Tallman & Tallman 1997), although even some birds which breed year-round will not breed and molt simultaneously (Chapman 1995). It is possible that the high incidence of breed-molt overlap in Singapore is due, in part, to slower feather replacement and longer molts. Most small birds replace their feathers once to twice per year (Rower 2009). Primary molt takes approximately 16 weeks for Yellow-vented Bulbuls (*Pycnonotus goiavier*) in Singapore, which is slower than the 10–12 weeks often seen at higher latitudes (Ward 1969). It may be the case that slow aseasonal molting is possible, because there is less of a need for strict molt scheduling among non-migratory birds, especially at sites where food availability is fairly stable throughout the year. The fact that breeding is seasonal, while molt is not opens the possibility that in this case birds may breed seasonally for the sake of reproductive synchronization rather than to take advantage of increased resource availability, considering that both molt and reproduction are energetically costly.

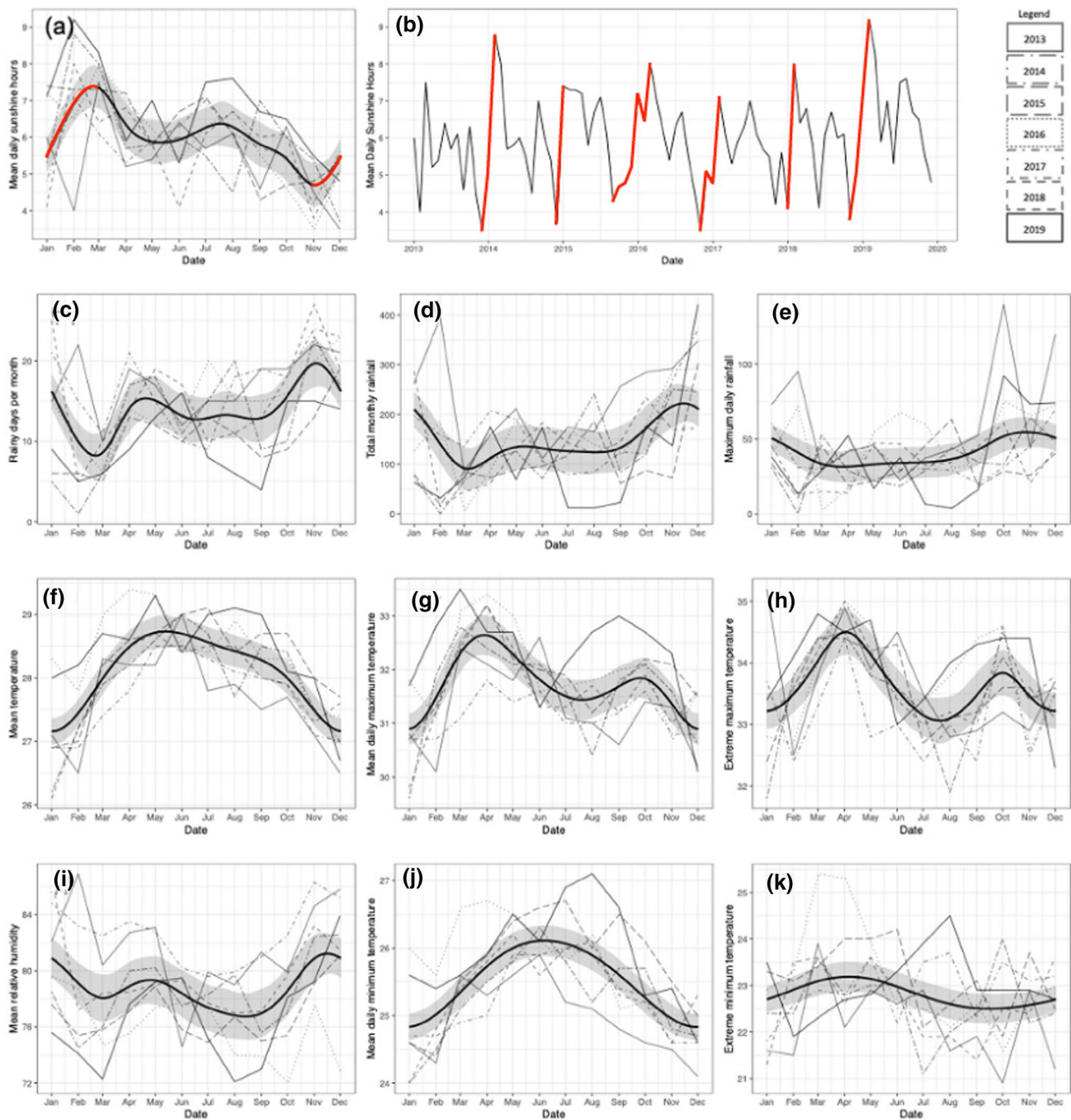


Fig. 7 Cyclic spline basis generalized additive models of climatic variables collected at Changi Climate Station from 2013 to 2019 based on data from Singapore National Environmental Agency (from data.gov.sg/group/environment). Trend lines show values from individual years. **a–b** Mean daily sunshine hours, **c** rain days per month,

d total monthly rainfall, **e** maximum daily rainfall, **f** mean temperature, **g** mean daily maximum temperature, **h** extreme maximum temperature, **i** mean relative humidity, **j** mean daily minimum temperature, and **k** extreme minimum temperature. Red color emphasizes increase in mean daily sunshine hours in Nov–Mar of each year

Fluctuations in food availability are consistent with breeding seasonality

Insectivores and frugivores in Singapore breed at the same time of year, while granivores may or may not have

a slightly offset breeding season. No independent assessment of fruit, insect, and grain abundance was conducted for this study, but previous studies have outlined the seasonal changes in abundances. Ward (1969) suggests that insects are plentiful throughout the year, but may be most

Table 1 Climate and breeding seasonality among multiple relevant studies. Colors correspond with values for rainfall (wettest=green, driest=red) and temperature (hottest=red, coldest=blue)

#	Article	Site	Köppen climate classification	Latitude	Rainfall (mm)		Temperature (°C)		Breeding
					wettest month	driest month	hottest month	coldest month	
1	Auer et al. 2007	El Rey National Park, Argentina	CWB - Subtropical highland climate	-26	176	3	21.7	10.7	Seasonal, early rainy season
2	Dittami 1987	Lake Nakuru National Park, Kenya	CSB - Warm summer mediterranean climate	-0.4	129	26	18.7	16.4	One species seasonal, one species aseasonal
3	Brandt & Creswell 2008, Cox et al. 2013	Amurum Forest Reserve, Nigeria	AW Tropical wet and dry / savannah climate	9.9	298	0	25.7	20.9	Seasonal, late rainy season and start of dry season
4	Diamond 1974	Kingston, Jamaica		18	182	24	27.7	24.8	Seasonal, early rainy season
5	Wikelski, Hau and Wingfield 2000	Soberanía National Park, Panama		9	293	11	28.1	26.3	Seasonal, rainy season
6	McClure 1974	Khao Yai National Park, Thailand		14.4	312	6	30.1	25.4	Seasonal, nesting Jan-May
7	Serle 1981	West Cameroon	AM Tropical Monsoon Climate	4	681	39	27.4	24.4	Breeding occurs seasonally in the mountains and year-round in the lowlands. Most species have no distinct breeding season
8	Bates 1908	South Cameroon		2.8	484	68	26.9	24.3	
9	Komdeur 1996	Seychelles Islands	AF Equatorial tropical rainforest climate	-4.3	364	65	27.4	25.6	Seasonal on Cousin island, aseasonal on Aride island
10	Tallman & Tallman 1997	Limoncocha, Ecuador		-0.4	327	174	25.9	24.3	Aseasonal
11	Fogden 1972	Semengo forest reserve, Sarawak, Malaysia		1.4	669	194	27.8	26	Seasonal, brood patch in March
12	This study	Singapore		1.3	317	104	28.4	26.6	Seasonal, nest in March

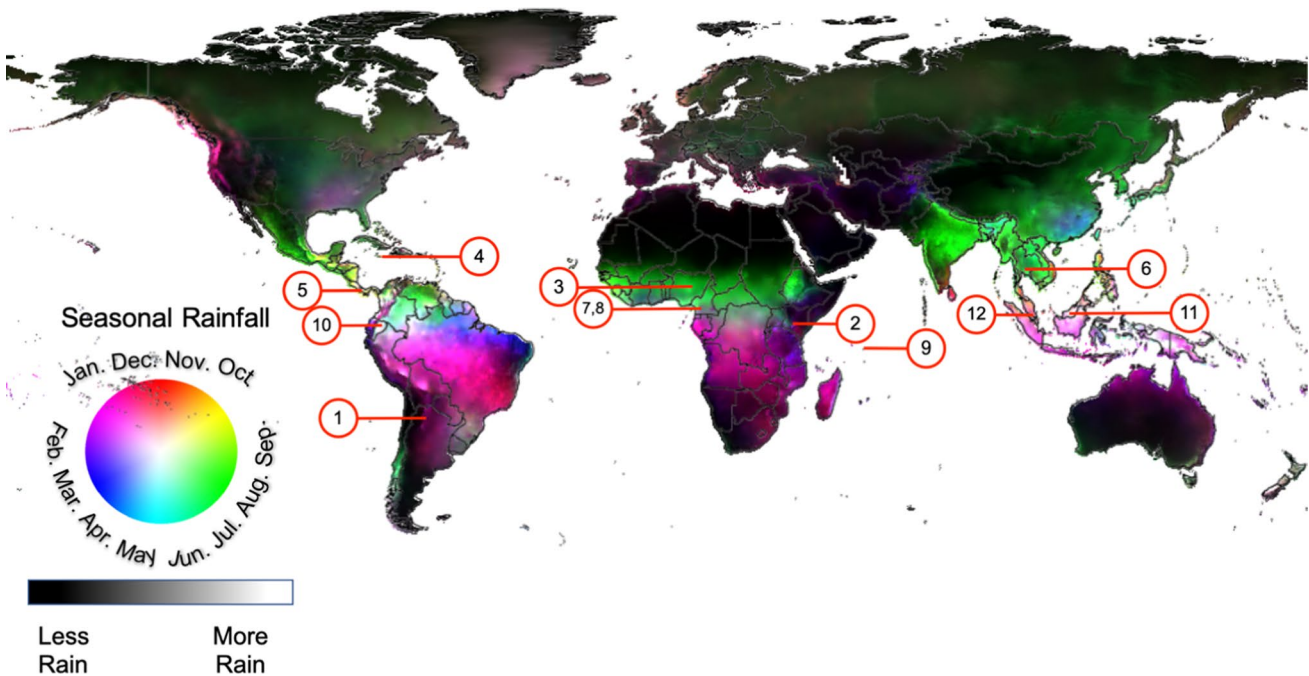


Fig. 8 Global seasonal rainfall map with red–green–blue false color, in which red indicates rainfall in October–January, green indicates rainfall in June–September, and blue indicates rainfall in February–

May. Brighter colors indicate higher rainfall, while darker colors indicate less rainfall. Circled numbers refer to study sites in Table 1. Raster data were obtained from WorldClim.org

numerous in January–July, although this seasonal increase is small in comparison to monsoonal and temperate regions. The abundance of insects during the most plentiful month may be about double that of the least plentiful month (Ward

1969), but recent multi-year data on actual insect abundances are lacking. In general, fruit availability is constant throughout the year, with irregular masting events occurring every 1–9 years. Figs, a staple of the frugivorous diet, fruit

irregularly on the individual level but continuously on the population level and provide a reliable year-round food supply (Cannon et al. 2007; Corlett 2019). Other common genera of bird-dispersed fruit-bearing plants, including *Litsea*, *Myristica*, *Santiria*, and *Timonius*, follow a masting pattern of reproduction (Corlett 1990).

The dietary guilds of the species in this study are not exclusive: species which are primarily frugivorous will also eat insects and vice versa. Both insectivores and frugivores feed insects to their young due to the high protein content. An insectivorous diet allows fledglings to grow more rapidly and become independent more quickly (Medway and Wells 1976; Morton 1973). Higher insect abundance during the first half of the year would coincide with the breeding season and it is possible that the timing could be adaptive to take advantage of higher food availability.

Recent major masting events in Singapore occurred in 2001, 2005, 2009, and 2014 (Chong et al., 2016). Masting events are typically triggered by an extremely dry February, with general flowering occurring in May and mass fruiting occurring in July (Corlett 1990, 2019). There was a mass fruiting event in 1987 from late June–August (Corlett 1990), and the mass fruiting event in 2014 occurred over 8 weeks in July–August (Chong et al., 2016). The 2014 glut of fruit did coincide with the typical peak fledging period of the breeding season. Fledging is the stage of the breeding season with the highest demand for food—when parents are required to provide food for dependent young. It is intuitive that an alignment between breeding season and masting events would be adaptive. Given the inherently stochastic nature of masting events, it is unclear how strong of a driver they would be for the regular timing of annual breeding seasons, but the magnitude of the benefit of breeding during a masting event may be sufficient to affect reproductive timing despite the fact that such events do not occur in all years.

There was not enough data to fully characterize the granivore breeding season (Fig. 3c). Grassland habitat in Singapore is non-native and exclusively of anthropogenic origin, and is comparatively uncommon, so there are few species of granivores. The majority of granivore nesting observations were of one species with a highly conspicuous nest (Baya Weaver *Ploceus philippinus*). Therefore, it is unclear whether the sharper and later peak in nesting observed among granivores represents a true difference or whether it is an artifact of the small sample size.

The possibility of migrant avoidance

While food availability is thought to be the primary driving factor behind seasonal breeding in most studies, it is important to consider other possible factors. Competition between visiting migrants and resident species has been suggested as a cause of breeding seasonality in the Neotropics

(Miller 1963), although no strong evidence has been published in favor of this hypothesis. In our study, migrant presence did correlate negatively with the breeding season. The number of migrant birds present in Singapore was at an absolute minimum when resident birds were fledging (Fig. 4). It could be possible to argue that migrant competition may play a role in the timing of the breeding season in Singapore. However, migrant competition is generally not accepted as an ultimate driver of breeding seasonality (Moreau 1950; Thomson 1950), because the correlation between the absence of migrants and resident reproductive activity is not maintained across geographical regions. In tropical Africa (Moreau 1950; Thomson 1950), some areas in Thailand (McClure 1974), and other parts of Southeast Asia (Medway and Wells 1976), many resident birds breed at the time of year when visiting migrants are most abundant.

Number of sunshine hours is most likely trigger of breeding

As an observational rather than experimental study, it was possible to show relationships between variables but not to prove causality. That said, the use of multi-year data can rule out certain variables as potential proximate triggers. The breeding season occurred at the same time across all 6 years, so the triggering factor or factors which act to maintain regular seasonality must have followed the same annual predictable pattern. Since nesting, the first stage of the breeding season, begins to increase in November and December, the triggering event likely also occurs at that time of year or slightly before. While the number of rainy days per month, maximum rainfall in a day, and total monthly rainfall are on average highest in November and December, there is no threshold minimum amount of rainfall that falls only during those months and no other time of year (Fig. 7c–e). The mean number of sunshine hours shows a clearer annual pattern (Fig. 7a–b).

It is possible that the average daily number of sunshine hours may have a regulatory effect on breeding season. Most birds use photoperiod to regulate seasonal behaviors (Cassone and Yoshimura 2015). However, at tropical latitudes, photoperiod varies little, and true photoperiod can be obscured by cloud cover and rainfall, which influence the effective number of sunshine hours (Medway and Wells 1976). In Singapore, true photoperiod varies by only 9 m throughout the year, but effective daily sunshine hours can vary by as much as 4–6 h throughout the year due to higher cloud cover during November and December (Fig. 7a–b).

Some species of resident tropical birds are known to respond to photic cues, even though there is little variation in photoperiod in their natural habitat (Beebe et al. 2005). To the best of our knowledge, the smallest change in photoperiod experimentally known to induce breeding condition

is 17 min (Hau et al. 1998). While Singapore's true photoperiodicity is well below this 17 min threshold, the effective variation in sunshine hours is well above it. In Singapore, the seasonal modulation in effective sunshine hours is fairly reliable from year to year (Fig. 7). In all 6 years of this study, there was a sharp increase in mean daily sunshine hours from November until February, when residents begin to nest, which might be loosely compared to the springtime increase in photoperiod seen at higher latitudes. There were fluctuations in mean sunshine hours at other times of year, but those fluctuations were always smaller than the 3.5–5.5 h increase in average daily sunshine hours that occurred from November to February. It is unclear how well sunshine hours could act as a triggering factor considering the large amount of stochasticity in the seasonal trend, but it is an appealingly parsimonious explanation, considering that photic cues are used to coordinate phenological events among most species of birds. Future research may be able to model the relationship between these variables with more precision.

Previous publications have hypothesized that both photoperiod and rainfall act as regulating factors for the breeding season in equatorial Southeast Asia (Gibson-Hill 1952), but have not proposed a biological mechanism which allows rainfall patterns to influence hormone balances which induce reproductive behavior. Sunshine hours correlate with both photoperiod and rainfall, and reconcile the modulatory effects that different climatic variables can have upon subjective photoperiodicity. It is possible that at sites where birds are currently believed to schedule their breeding according to rainfall, a change in average daily sunshine hours due to cloud cover and rainfall may act as the triggering factor in reproductive scheduling instead.

The number of sunshine hours appears to be a powerful predictor of seasonality in other equatorial regions. In West Cameroon, lowland and montane habitats share the same photoperiod and seasonal rainfall patterns, but at montane elevations, where breeding is seasonal, a thick mist forms during the rainy season and significantly decreases light intensity, while in the lowlands, where mist clouds do not form, breeding occurs year-round (Serle 1981). Tropical resident populations may have a photosensitive response to seasonal fluctuations in sunshine hours caused by overcast weather despite a very small seasonal variation in true photoperiod.

Limited support for body condition as a regulator of breeding activity

Ward (1969) hypothesized that body condition could act as a biological oscillator regulating the timing of the breeding season. According to this hypothesis, birds will not breed until their body condition is good enough to breed successfully. During the breeding season, the strain of egg

production, nesting, and parental care leads to an overall decrease in muscle and fat reserves. After the breeding season ends, body condition gradually improves. When food availability increases at the beginning of the year, body condition becomes strong enough to trigger the onset of breeding. This hypothesis is appealing, because it allows food availability to act as both a driver and a trigger for seasonal breeding, but our data do not fully support it.

Average PEC score, a measure of body condition, did display a cyclic seasonal pattern corresponding with the breeding season. In all 6 years, average PEC score decreased over the course of the breeding season and recovered during the non-breeding season. However, in order for body condition to act as an effective trigger, all breeding individuals would need to reach a certain maximum body condition at the beginning of the breeding season. While the number of individuals in excellent body condition was highest at the onset of the breeding season each year, the majority of individuals still exhibited an average body condition, and many individuals in excellent body condition continued to be found throughout the year. If body condition did act as a trigger for the onset of breeding, then we would expect to see many more individuals breeding outside the season characterized here. Body condition is likely negatively affected by the strain of breeding, and a better body condition may increase the likelihood of successful breeding, but it is unlikely that it acts as a proximate factor in initiating the breeding season in this case.

Conclusion

In Singapore, the onset of the breeding season corresponds with an increase in subjective sunshine hours. It is likely that the timing of the breeding season is regulated by a photosensitive response to seasonal fluctuations in sunshine hours caused by overcast weather in November and December, despite a very small seasonal variation in true photoperiod. Resident birds breed at a time that may correspond with increased insect availability, higher likelihood of overlap with masting events, and the absence of migrants. Any one of these variables, or a combination thereof, may contribute toward the adaptive advantage of breeding according to the observed seasonal pattern.

The phenological dynamics of most species in tropical ecosystems are still poorly understood, especially in Southeast Asia. Understanding the role that climatic factors play in regulating the reproduction of these species is critical to predicting how climate change might impact the stability of already threatened populations. Knowledge of local breeding seasons also has the potential to aid conservationists by allowing protection efforts to be prioritized during the most critical times.

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Author contributions All authors contributed to writing the paper. LB formulated the question, developed methods, and analyzed the data. DL and YS contributed NParks mist-netting records. MK vetted and curated eBird records. FR contributed NUS mist-netting records and supervised research.

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Data availability Raw data presented in this article is available at <https://doi.org/10.5061/dryad.k3j9kd5b5>. Citizen science records were obtained from and are available at eBird.org.

Declarations

Conflict of interests The authors declare that there is no conflict of interest.

Ethical approval NParks facilitated field work under permits RP13-019-2, RP13-019-3, RP13-019-4, RP13-019-5, and RP13-019-6. Field work was conducted in compliance with NUS's Office of Safety, Health and Environmental regulations and with approval from the NUS Institutional Animal Care and Use Committee.

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