The effect of elevation on the timing of the dawn chorus

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Abstract

Due to rising temperatures driven by climate change, the daily rhythms of the Australian Alps are undergoing profound shifts, impacting a diverse array of species and their behaviours. The 'dawn chorus,' a natural symphony where birds unite in melodic harmony in the early morning, is falling out of sync due to evolving environmental cues, notably temperature and light. This study addresses the question of whether the dawn chorus initiation time varies with elevation and explores the hypothesis that bird routines are tied to the availability of food resources. Our findings assessing the calls of the grey fantail, *Ripidura albiscapa*, derived from autonomous recordings at four sites along an elevational gradient and taking temperature into account, consistently reveal a delayed start to the dawn chorus at higher elevations, with an associated decrease in average temperature. These results not only illuminate the complex interplay between elevation, temperature and the dawn chorus, but also underscore the far-reaching implications of climate change on the delicate rhythms of nature.

Running Title: Variation in dawn chorus timing with elevation

Key Words: temperature, behaviour, light, behavioural ecology, circadian rhythms

Introduction

Disturbance ecology is characterised by the rate and magnitude of behavioural change among species and can be linked to spatial variables such as temperature and elevation (Graham *et al.* 2021). Temporal patterns, like the dawn chorus, reflect the interactions between species and their environment (Pérez-Granados *et al.* 2018). Environmental conditions such as temperature and elevation can affect the time when birds start singing in the morning (Pérez-Granados *et al.* 2018). Such environmental impacts lead to changes in life history traits, movement patterns and behavioural habits on a time scale that can be displayed daily, seasonally or yearly (Burt & Vehrencamp 2005). Examples of these changes can be observed in key singing behaviours (Burt & Vehrencamp 2005).

Circadian rhythms – the body's internal clock – cycle through 24-hour behavioural patterns (Turek 1978). Birds rely on these rhythms to measure day length and regulate their responses to light (Turek 1978). Diurnal cycles, driven by Earth's rotation, include abiotic (temperature changes) and biotic (animal feeding and communication) components (Leveau 2018). Interaction between these components is vital for understanding animal behaviours and their influencing variables (Leveau 2018).

The dawn chorus is an example of a diurnal cycle observed in bird communities. It is the daily ritual of territorial individual birds in a neighbourhood to sing in sync 30–90 minutes before sunrise (Pérez-Granados *et al.* 2018). The singing is not a form of interaction between one bird and its neighbour, but rather a singing together of all of the birds in a neighbourhood, which creates the highest complexity of song (Burt & Vehrencamp 2005). Once the sun has risen and light levels have increased, the chorus of birdsong ends (Burt & Vehrencamp 2005). The chorus's abrupt end aligns with the time when the birds begin to search for food and protect their borders, switching to dyadic singing, or singing to neighbours (Pérez-Granados *et al.* 2018).

Explanations of the dawn chorus phenomenon generally address one or the other of two distinct but essential questions: Why do many birds sing simultaneously? Why do they choose to do so early in the morning? We focused on the second question and explored some of the many hypotheses accounting for environmental reasons for the dawn chorus that have been proposed (Staicer *et al.* 1996), along with their implications for elevation.

Among the environmental hypotheses that attempt to explain why birds sing early in the morning, one key proposition is the 'acoustic transmission hypothesis' (Staicer *et al.* 1996). This theory suggests that the morning hours offer better acoustic transmission conditions (Staicer *et al.* 1996). At this time of day, there is less ambient noise, allowing birds to sing more loudly and have their songs carry over longer distances (Staicer *et al.* 1996). This hypothesis aligns with the idea that singing in the early morning is an effective means of long-distance communication (Staicer *et al.* 1996). If this hypothesis were to take into account changes in elevation, it might suggest that birds at higher elevations may not need to sing as early as birds at lower elevations, because there might be less noise interference at higher elevations, leading to different singing patterns.

Another environmental hypothesis is that of 'energy storage stochasticity', according to which birds aim to store more energy than they need overnight to enhance their chances of survival (Burt & Vehrencamp 2005). The stored energy can be used for morning song when foraging or hunting is hindered, possibly due to harsh environmental conditions (Burt & Vehrencamp 2005). If this hypothesis were to account for elevation, it might predict that birds at higher elevations, facing potentially harsher conditions, would prioritise energy conservation and, therefore, start singing earlier.

Lastly, the 'inefficient foraging hypothesis' connects light availability with the dawn chorus, and suggests that birds begin their morning song when light is scarce because it is inefficient to search for prey in low-light conditions (Berg *et al.* 2006). Earlier light availability would predict an earlier dawn chorus (Berg *et al.* 2006). Therefore, this hypothesis hints that birds at higher elevations, which might experience different light conditions to birds at lower elevations, could have different singing schedules depending on their foraging efficiency.

We studied the grey fantail, *Ripidura albiscapa*, a common aerial insectivore that is noticeable at most elevations in Kosciuszko National Park (Munro 2007). It also produces one of the first calls noticeable in the morning at most altitudes in our study area. The grey fantail is a partly migratory passerine flycatcher that feeds primarily on flying insects and is found throughout Australia, most commonly in woodlands (Munro 2007).

We hypothesised that aerial avian insectivores at higher elevations would commence their morning songs later than those at lower elevations. This prediction stems from the temperature dependency of insect activity (Mellanby 1939): as elevation influences temperature, food resources become available to insect-eating birds at higher elevations later.

Methods

Sample collection

To conduct this observational study, four bioacoustic audio recorders (BAARs) and associated HOBO data loggers were placed at different elevations in the Kosciuszko National Park. The study sites were Sawpit Creek (elevation, 1,200 m), Wilsons Valley (1,476 m), Rainbow Lake (1,612 m) and Charlotte Pass (1,817 m). The recorders and data loggers were set to record the dawn chorus along with temperatures and light levels in the associated areas between 4 am and 6 am over the four days from 4 December until 7 December.

All four recorders were placed in woodlands near streams to allow for consistency between elevations. Stream noise overrode every recording; to remove this, we used noise reduction in Audacity. HOBO data loggers were left with each recording device to measure temperature. Temperature was measured for three days. There were two rainy days at Sawpit Creek and Rainbow Lake, which seemed to impact the first call times, and therefore rainy days were considered different data and were not included in our results (Figure 4).

The digital audio editor and recording application Audacity was used to identify the recorded calls. The two prominent calling birds in all four areas were the flame robin and the grey fantail. The grey fantail's calls were used for further analysis, as the grey fantail was the first bird to call and was the most distinguishable. Grey fantails are also aerial insectivores, so their foraging efficiency is affected by temperature and elevation, the factors we used in comparing calling time (Bain *et al.* 2020; Webb-Pullman & Elgar 1998).

We decided to use the first call of the grey fantail as the factor being measured between the four sites and in relation to elevation and temperature. To distinguish this call in Audacity, we imported the audio files produced by the four recorders into the software and interpreted the recorded sounds on a spectrogram that plots frequency against time (Figure 1). We identified the first call by its unique Graph Fourier transform (GFT) pattern and noted the time when it occurred. The grey fantail's call is high and clear, with a frequency of roughly 5,000–6,000 Hz, making it an easily distinguishable call, especially compared to the calls of other bird species in the vicinity. In addition to the time of the first call, we also noted light level.

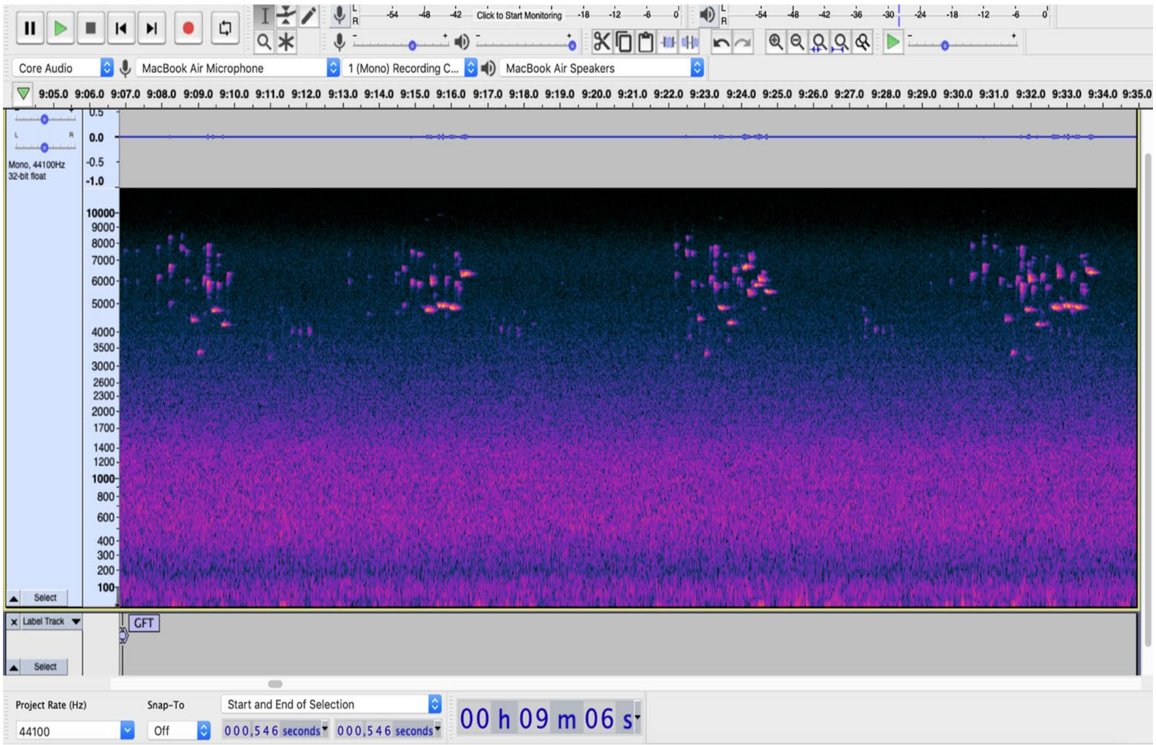

Figure 1: *Spectrogram showing the grey fantail calling pattern displayed in Audacity, with frequency in Hz of the bird call on the y-axis and time of call on the x-axis. The melodic patterns of four instances of the grey fantail's call can be seen in this frame.*

Audacity's spectrogram allowed us to identify the grey fantail's call by its frequency and complexity (Figure 1). Calls were detected by listening to the recording while looking at the spectrogram. Four people re-coded the days and sites to allow for faster identification. The re-coding was done so that scorers did not know which site a recording came from. The data were blind with respect to elevation of recording.

Data analysis

We used SPSS to analyse the data. The analysis uses a 'mixed model' that takes into account repeat measures at each site (random effect = day). It excludes data from rainy days.

$$Mean: \ \mu = \frac{\Sigma(\chi i)}{N}$$

Mean was used to average out the calling times in each site over the four days and the temperatures of all sites over the three days of temperature measurement.

$$Standard\ deviation: \ \sigma = \sqrt{\frac{\Sigma(\chi i - \mu)^2}{N}}$$

Results

As elevation increases, temperature decreases (Figure 2). Following this downward trend tells us that elevation is a suitable proxy for decreasing temperature.

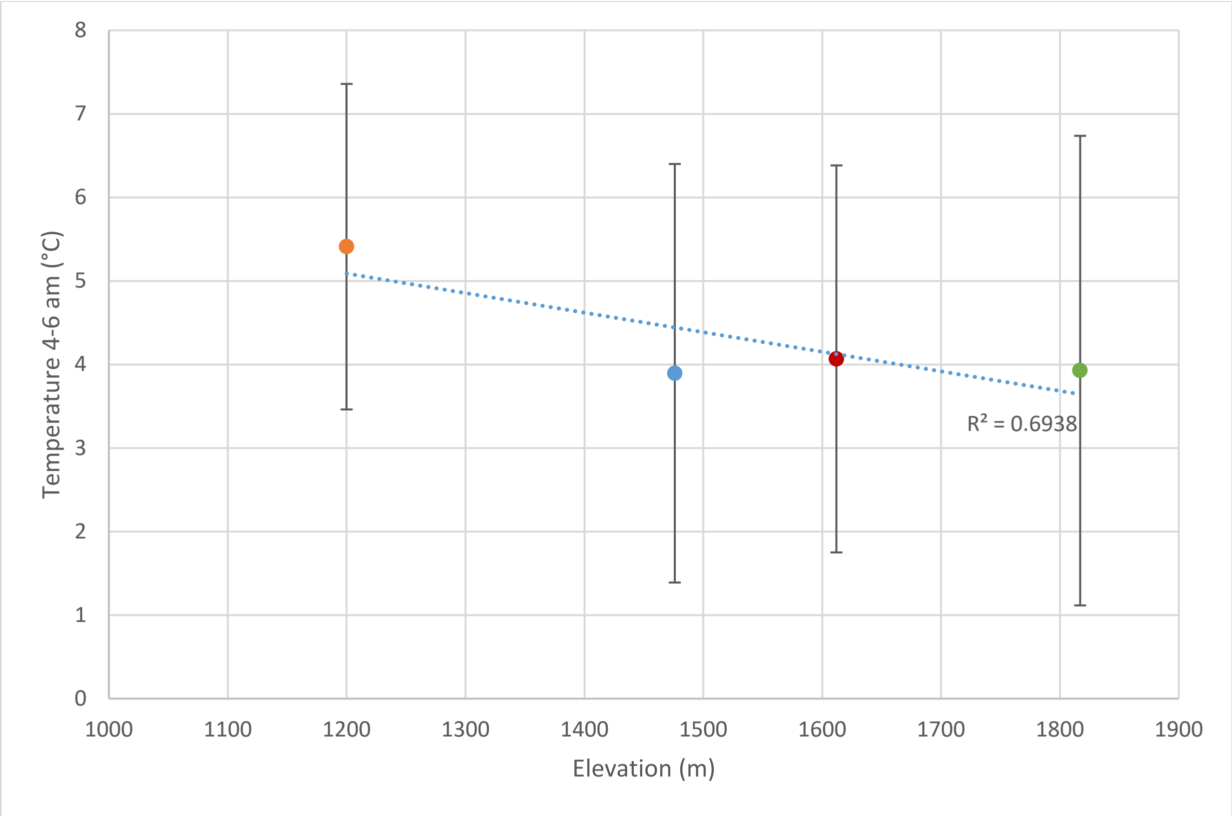

Figure 2: As elevation increases, temperature decreases. This figure shows us the relationship between temperature and elevation. The orange point represents Sawpit Creek (1,200 m), *the* blue Wilsons Valley (1,476 m), *the* red Rainbow Lake (1,612 m) and *the* green Charlotte Pass (1,817 m). The lowest elevation was 1,200 m and the highest was over 1,800 m. The lowest temperature reached approximately 2˚C and the highest was above 6˚*C* in the early hours of the morning (4–6 am). Error bars represent standard deviation from the mean of the data. R^2 = 0.6938*, indicating that* the points are closer to the trend line*;* a value of 1 would mean *it fits* exactly.

The average time of first call of the grey fantail varies across our four sites with different elevations (Figure 3). There is quite a strong positive trend, with birds down at Sawpit Creek starting to call just after 4 am, whereas up in Charlotte Pass they started after 5 am and closer to sunrise. In the middle two sites, the time of call is much more similar, likely due to their similar elevations. Statistical tests showed that these results were highly significant, with the p value being less than 0.001 ($F_{3,6} = 114.46$, $p < 0.001$). The F value is large, meaning great variances between points; however, our results support the hypothesis that fantails will call later at higher elevations.

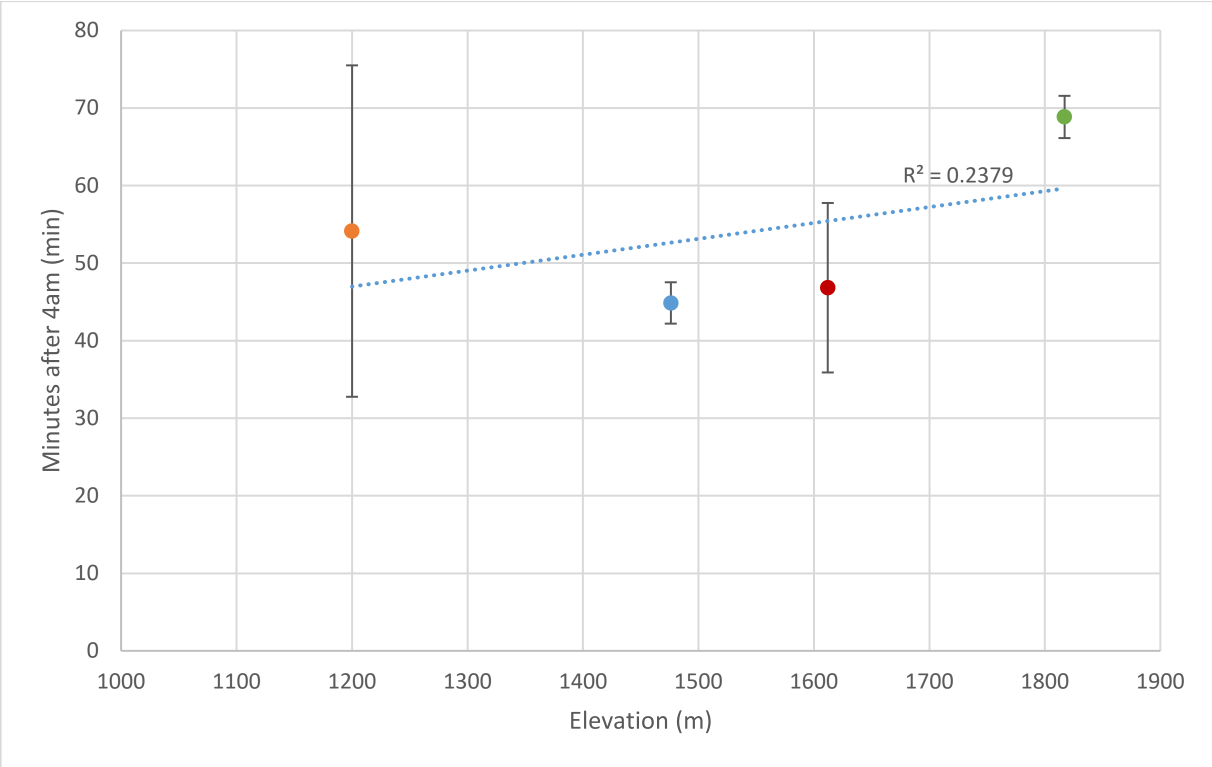

Figure 3: *An increase in elevation results in the time of first call being later. This graph represents the effect of elevation on the grey fantail's first calling time. The orange point represents Sawpit Creek (1,200 m), the blue Wilsons Valley (1,476 m), the red Rainbow Lake (1,612 m) and the green Charlotte Pass (1,817 m). Error bars represent standard deviation from the mean of the data.* $R^2 = 0.2379$*, indicating that the points are further from the trend line.*

On the days when it was raining – that is, days 1 and 2 at Sawpit Creek and Rainbow Lake (Table 1) – the time of the first call of the grey fantail was much later than on days when it was not raining. At Sawpit Creek when it was raining, the first call time was up to 70 minutes after 4 am, whereas when it was not raining the first call time was approximately 15 minutes after 4 am – a 55-minute difference. At Rainbow Lake when it was raining, the first call time was approximately 60 minutes after 4 am, whereas when it was not raining the average first call time was approximately 35 minutes after 4 am – a 25-minute difference.

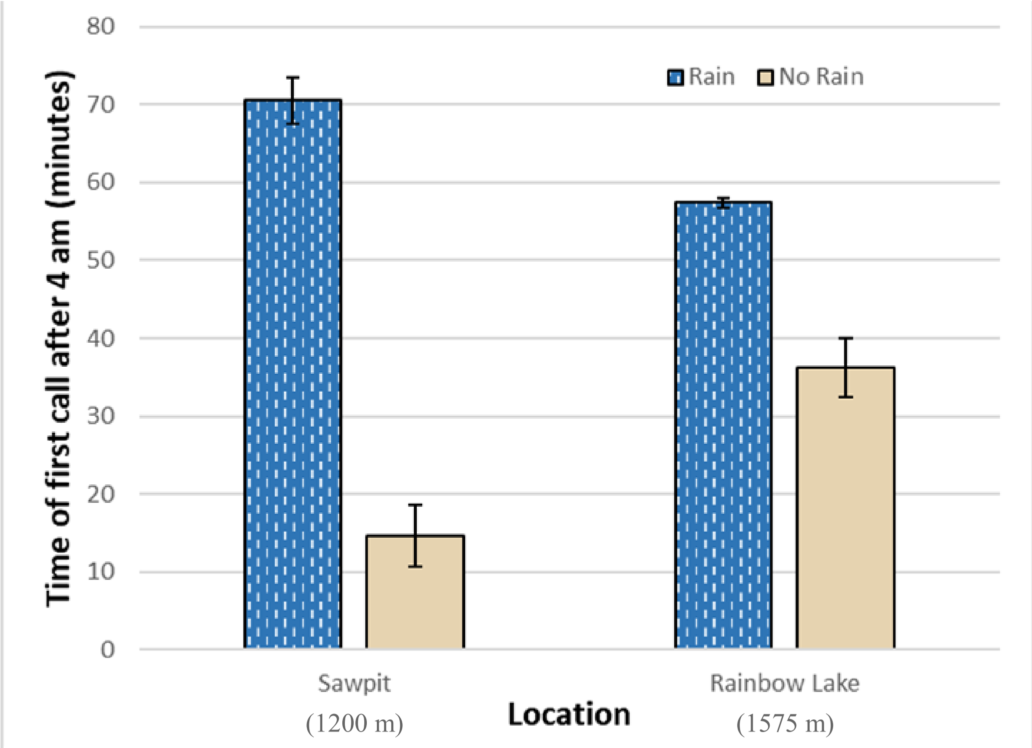

Figure 4: *Later first call* on days when it was *raining compared to* on days when there was *no rain.* The b*lue bar graph is rain*; the *beige bar graph is no rain*. I*t only rained at two locations over all four mornings of recording – Sawpit* Creek *(1,200 m) and Rainbow Lake (1,575 m). Bars depict means ± standard deviation.*

Discussion

The elevation and temperature of the grey fantail's habitat were found to affect the bird's first time of call. Thus, our results supported our hypothesis that as elevation increases the first call time of the grey fantail becomes later. This is clearly shown in Figure 3, with Sawpit Creek at the lowest elevation (1,200 m) and Charlotte Pass at the highest (1,817 m), and both Wilsons Creek and Rainbow Lake being of the same elevation (around 1,500 m). The standard errors and means suggest that this pattern is most likely driven by the high elevation data (Charlotte Pass), as the mean is high with a small standard error. Higher elevation serves as a reliable proxy for lower temperature (Figure 2), which, in turn, impacts species inhabiting the area. Lower temperatures create less optimal conditions for breeding and feeding, resulting in reduced species diversity, including insect populations – the primary food source for birds like the grey fantail. This elevational effect likely arises from the temperature's influence on insect activity and, consequently, the availability of food for avian insectivores.

The observed elevation-related effect aligns well with the prey availability hypothesis, which suggests that colder morning temperatures will delay the activity of aerial insects, a vital food source for birds like the grey fantail, making them less accessible until later in the day. The elevation-related effect also supports the energy storage stochasticity hypothesis, which suggests that birds will aim to store more energy than required overnight to heighten their chances of survival, due to unpredictable energy requirements and environmental conditions (Burt & Vehrencamp 2005). This excess energy is then used the following morning for song, while birds do not have the capacity to forage or hunt due to obstacles such as harsh environmental conditions, thus supporting the idea that birds at higher elevation in colder climates call later.

The trend of later call times at cooler temperatures might be explained by the pattern of generally higher insect presence at lower altitudes (Dostálek *et al.* 2018; Taylor 1963; Rokaya *et al.* 2016), which means that at a lower altitude, there would be a higher number of insects, even at earlier hours when insects may be less active. Because of this correlation, grey fantails may sing at earlier hours in lower elevations because they have adapted to hunting at an earlier time due to the greater availability of prey, while the lower availability of prey at higher elevations inclines grey fantails to wait until later when temperatures increase and insect activity increases.

When there is rain, grey fantails will tend to sing at a later time than if there is no rain at the same location (Figure 4), which suggests the timing of grey fantail singing is at least partially influenced by rainfall. One possible explanation for this is that when there is rain, certain types of flying insects like pollinators, which grey fantail feed on, are less likely to fly out to seek nectar, as rainfall will both cause degradation in nectar quality (Lawson & Rands 2019) and disrupt flying insects' sensory abilities (Lawson & Rands 2019). Because the grey fantail's diet is primarily flying insects, it is possible that because rainfall reduces the numbers of these insects in the air and thus the availability of prey during the time when grey fantails would usually be hunting, the grey fantails choose to sing later.

Our findings are indicative of an elevation effect – and therefore the temperature effect – on birds and their calls: at higher elevations and in colder climates, there will be fewer bird species due to there being less prey. This finding highlights the need for better understanding of bird interactions and calls in relation to essential behaviours such as mating and eating, and to patterns of energy expenditure throughout the day.

More studies and experiments could be carried out to further understanding of the dawn chorus. For example, since rain is a primary factor affecting the timing of the dawn chorus, periods of rain could be compared with periods of no rain across sites, to facilitate deeper understanding of rain's impact on timing of the dawn chorus at different elevations. In this study, there was no replication of sites at any given elevation; including such replication in a future study could improve validity. A focus on the correlation between insect population and bird population, and how it affects the timing of the dawn chorus, would allow us to look more directly at the prey availability hypothesis. To understand the dawn chorus in its entirety, it would be necessary to look at variations among all of the songbirds and the reasons for the differences in the timing of their calls.

Conclusions

This study underscores the tight links between elevation, temperature and grey fantail behaviour, revealing that as elevation rises, these birds delay their morning calls. This aligns with the prey availability hypothesis, as higher elevations often mean colder morning temperatures that hinder the activity of insects, the primary food source for grey fantails. This elevational effect also supports the energy storage stochasticity hypothesis, indicating that birds conserve energy until more favourable foraging conditions emerge later in the morning. Additionally, we observed that rainfall prompts grey fantails to sing later, possibly due to reduced insect activity during inclement weather. Our findings provide valuable insights into the intricacies of bird behaviour in response to environmental variables, shedding light on the dynamics of avian life in diverse ecosystems.

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