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ORIGINAL ARTICLE

Do the rain calls of Chaffinches indicate rain?

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Abstract

For more than 300 years, the rain call of the Common Chaffinch (*Fringilla coelebs*) has been thought to herald rain—hence the name. However, the biological function of this vocalisation still remains unknown. Because rain calls are produced only by males during the breeding season, it has been suggested that the call serves a territorial function and that it may replace song in adverse situations, such as bad weather. However, it is unclear whether rain calls are linked to precipitation at all. Here, we explored the relationship between the occurrence of rain calls and the weather, based on the hypothesis that rain calls are produced instead of song during rainfall. For that purpose, we conducted three studies on different geographical and temporal scales: a large-scale analysis across Europe (relating 242 audio recordings from the Xeno-Canto archive to weather data) and two observational studies in Germany (one cross-sectional study surveying 509 Chaffinches and one longitudinal study on 49 selected males over a period of two weeks). We found no association between rain calls and rainfall in any of the three datasets (but males tended to produce more rain calls with increasing cloud cover and wind force). However, the occurrence of rain calls varied markedly with the social context, as males were more likely to rain–call in the presence of a female, suggesting a function within the pair bond. Overall, we press for more studies on bird calls, and the rain call (although inappropriately named) appears to be a particularly interesting candidate.

Keywords Animal communication · Bird song · Bird call · *Fringilla coelebs* · Rain call · Weather

Zusammenfassung

Zeigt der Regenruf des Buchfinken Regen an?

Seit über 300 Jahren wird angenommen, dass der Regenruf des Buchfinken (*Fringilla coelebs*) Regen ankündigt. Die biologische Funktion dieser Lautäußerung ist allerdings nach wie vor unbekannt. Da Regenrufe nur von Männchen während der Brutzeit produziert werden, wurde vermutet, dass der Ruf eine territoriale Funktion hat und den Gesang in ungünstigen Situationen, wie z. B. bei schlechtem Wetter, ersetzen kann. Es ist jedoch unklar, ob Regenrufe überhaupt mit Niederschlägen in Verbindung stehen. In dieser Studie haben wir den Zusammenhang zwischen dem Auftreten von Regenrufen und dem Wetter untersucht, wobei wir von der Hypothese ausgingen, dass Regenrufe während des Regens anstelle von Gesängen produziert werden. Dazu haben wir drei verschiedene Datensätze auf unterschiedlichen geografischen und zeitlichen Ebenen erhoben: eine großflächige Auswertung von Audioaufnahmen aus Europa (in der 242 Aufnahmen aus dem Xeno-Canto-Archiv mit Wetterdaten in Beziehung gesetzt wurden) und zwei kleinräumigere Beobachtungsstudien in Deutschland (eine Querschnittstudie mit 509 Buchfinken und eine Längsschnittstudie mit 49 ausgewählten Männchen

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über einen Beobachtungszeitraum von zwei Wochen). In keinem der drei Datensätze konnten wir einen Zusammenhang zwischen Regenrufen und Niederschlag feststellen (allerdings tendierten die Männchen dazu, mit zunehmender Bewölkung und Windstärke geringfügig mehr Regenrufe zu produzieren). Das Auftreten von Regenrufen variierte jedoch deutlich mit dem sozialen Kontext: Die Männchen produzierten Regenrufe eher in Anwesenheit eines Weibchens, was auf eine Funktion innerhalb der Paarbeziehung hindeutet. Generell plädieren wir dafür, mehr Untersuchungen über Rufe durchzuführen–der Regenruf (obgleich unpassend benannt) scheint dafür ein besonders interessanter Kandidat zu sein.

Introduction

Songbird vocalisations are usually divided into calls and songs. Songs are learned, mostly complex, and seasonal vocalisations that function as mate attraction and territory defence, while calls are typically innate vocalisations with a simpler structure, are emitted in specific contexts, such as foraging, movement or predator-avoidance (Catchpole and Slater 2008). The proximate and ultimate causes of bird song production are well studied, at least in temperate regions (Slater 2003), but research on bird calls is seriously lacking (Marler 2004). Notable exceptions to this neglect are alarm and mobbing calls, with their crucial function for survival and the potential for inter-species communication (e.g., Templeton et al. 2005; Templeton and Greene 2007; Griesser 2009; Magrath et al. 2015; Dutour et al. 2021; Sandoval and Wilson 2022). The begging calls of nestlings have also received considerable attention in the past (Wright and Leonard 2007). Begging calls are particularly interesting because they may reflect the parent–offspring conflict (Trivers 1974; Kilner and Drummond 2007) and cost–benefit trade–offs (Moreno-Rueda 2010; Haff and Magrath 2011). Finally, food calls are used as a model to understand the evolution of referential signals (Bugnyar et al. 2001; Evans and Evans 2007). In many cases, however, the proximate causes that trigger call production remain unknown, as do the evolutionary functions of many calls. In other words, the role of calls in bird communication is still not well understood (Marler 2004). In this study, we investigate a particular call that has been well described in the literature, but its function still remains something of an enigma—the rain call of the Common Chaffinch (*Fringilla coelebs*).

Chaffinches are one of the most common passerine species in Europe (Payevsky 2020). They occur in forests and woodlands with tall trees as well as in gardens and city parks (Macleod et al. 2004). The vocal repertoire of the male Chaffinch includes one to six song types (Fig. 1a), and a variety of calls (in his pioneering study, Marler (1956) described eight different call types). The rain call (Fig. 1b) is probably the best studied of the Chaffinch calls. In many cases, the special interest in the rain call lay in its peculiar features that are reminiscent of song. For instance, the rain call comes in marked geographical dialects, sometimes at very small spatial scales (e.g., Poulsen 1958; Detert and Bergmann 1984; Baptista 1990; Skiba 2000), and the dialect is learned at the juvenile stage (Riebel and Slater 1998a). Also, only male Chaffinches rain–call and they do so exclusively during the breeding season (e.g., Heyder 1954; Marler 1956; von Haartman and von Numers 1992) from inside their territories (Saur et al. 1996), and rain–calling may follow a diurnal pattern (Skiba 2005). Chaffinches tend to react to rain–call playbacks by rain calling (Skiba 2005; Müller 2023), and they may increase the rain–calling activity after territory intrusion (Budka et al. 2019). However, the function of the Chaffinch rain call is still not fully understood.

Because of these song–like features, several authors have suggested that rain calls are emitted as a substitute to song when a male is exposed to cold and humid weather or in other unfavourable situations, such as the presence of predators, a lack of food or the absence of the partner (Sick 1939; von Haartman and von Numers 1992; Bergmann 1993). The origin of the term “rain call” can be traced back to a book from 1707 written by the ornithologist Ferdinand von Pernau, in which the author suggests that the call is linked to rainfall (von Pernau 1707; Thielcke 1988). However, the term (and hence the perceived connection with rain) might be even older; it was perhaps part of folklore for a long time before written records. Indeed, the notion of a Chaffinch call that is linked to rain is evident in several European languages (English: “rain call”, German: “Regenruf”, French: “cri de pluie”, Swedish: “regnsång”, Czech: “volání deště”). Despite this apparently common belief, only a few studies have tested the association between the rain call and the weather. Three publications concluded that the rain call is produced more often when it rains (Heyder 1954; Jakobs 1963; Kemme 1983), but three others failed to find evidence for such a connection (Groebbels 1957; Voigt and Bezzel 1961; Skiba 2005). While Skiba (2005) found no support for the rain hypothesis, he reported increased rain–call activity in windy conditions and during rapid weather changes. The limited conclusions that can be drawn from these conflicting results are further impeded by small sample sizes and, in many cases, the lack of statistical (or any quantitative) analyses.

To resolve this issue, we investigated the relationship between the emission of rain calls and songs in Chaffinches and the weather. In particular, since it is hypothesised that Chaffinches trade off songs to rain calls during rain, we measured the proportion of rain calls and songs across weather conditions. To this end, we used three different

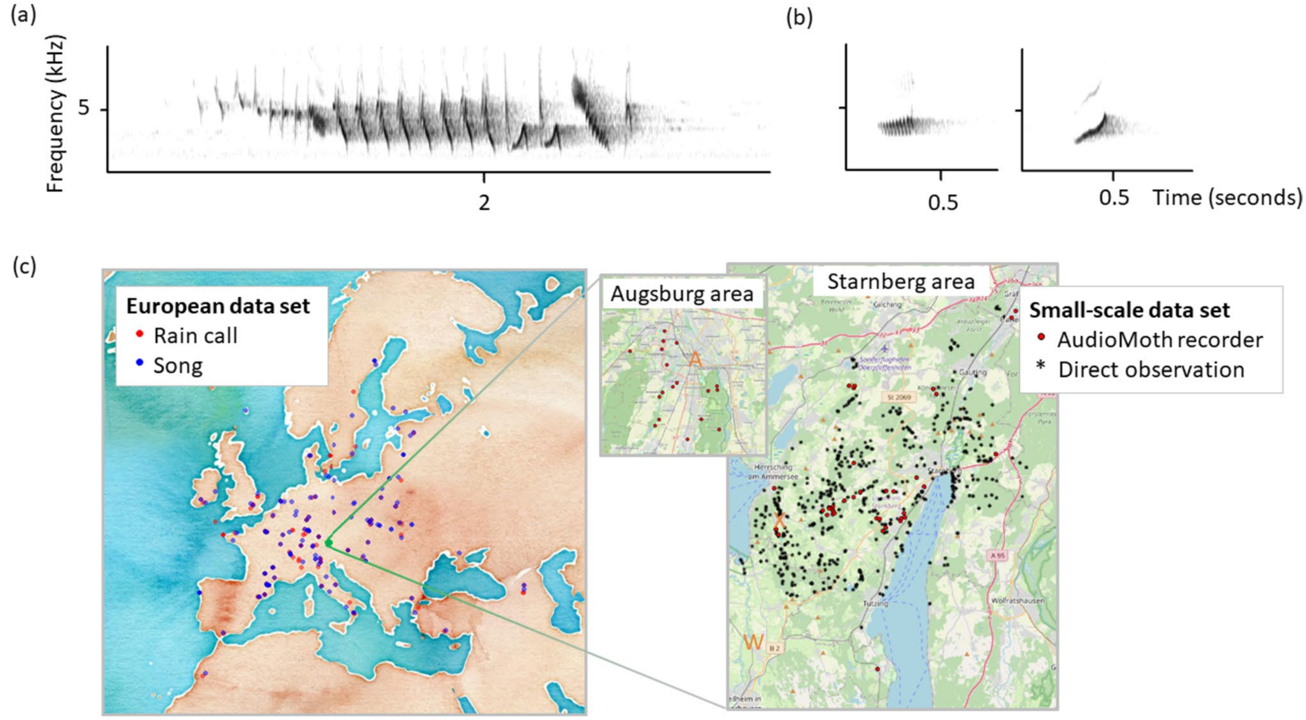

Fig. 1 Exemplary Chaffinch vocalizations and the spatial distribution of sampling in our three studies. **a** A Chaffinch song, **b** two different rain call dialects recorded in Bavaria, and **c** sampling locations. The locations of the weather stations are indicated with orange letters (A for Augsburg, W for Wielenbach, X for Andechs). Base maps from Stamen Design watercolor maps and ESRI streets, accessed through the R package *basemaps* v. 0.0.5

approaches: a large-scale data set based on recordings from Xeno-Canto and two small-scale data sets based on opportunistic and systematic recordings of Chaffinch vocalisations during the 2022 breeding season in Bavaria, Germany. By bringing together the findings from these three studies, we aimed to test the hypotheses that rain calls are emitted instead of songs in adverse weather conditions. We predict that the proportion of rain calls increases during rain or in relation to weather variable associated with precipitation (e.g., low atmospheric pressure, high cloud cover, high relative humidity). In addition, we investigated social variables that may trigger rain–call production. If the rain call has a similar function as song, we predict that the proportion of rain calls and songs does not change according to the social context.

Methods

We investigated the relation between the ambient weather conditions and the vocalisations of Chaffinches to understand whether the rain call is triggered by precipitation as the name suggests. Three separate data sets (Fig. 1) were used as independent tests, combining the strengths of different approaches: large (mainly Europe with a few additional data points from Africa and Asia) and small (Bavaria, Germany) geographic scales, as well as cross-sectional data (large sample size, weather varies between individuals, no repeated measures) and longitudinal data (smaller sample size, weather varies within individuals, repeated measures). First, we used the occurrence of rain calls and songs in a database of opportunistic bird recordings and paired this data with information from a weather data archive to establish the weather when the recordings were made. Second, we directly observed Chaffinches and noted the type of vocalisation together with the local weather. Third, we used automatic recorders to record the vocal activity of Chaffinches and the weather at constant points over longer time periods. In view of the hypothesis that the rain call may be a substitute for song, we compared the occurrence of rain calls to that of songs in all three approaches.

European data set

We used the application programming interface (API) from Xeno-Canto (https://xeno-canto.org/) on 11 January 2022 to search for recordings with the keyword “Fringilla + coelebs”. From the 5112 results returned, we extracted the recording time and date, latitude, longitude, and the description of the vocalisation. Then, we searched the vocalisation description ("file type", now called "othertype" in Xeno-Canto) for the keywords "rain", "rain call", "pluie", "regen", "*uit", and "rülschen" to select rain call recordings. We excluded recordings for which latitude and longitude or recording time were missing. We used the same methods using the keywords "song", "chant", and "Gesang" to select song recordings, and we excluded from the "song" dataset all recordings that also appeared in the "rain call" dataset to ensure independent sampling. Because highly unbalanced data sets induce bias in model parameter estimation (Salas-Eljatib et al. 2018), we balanced the number of song and rain-call data points by selecting the geographically closest song recording to each of the rain-call recording using the Euclidian distance of the GPS coordinates. Then, we listened to all the selected recordings to ensure that the song recordings did not contain any rain calls and vice versa.

For each recording location, we extracted the weather at the time of recording from the ERA5-Land hourly dataset (Muñoz Sabater 2021), available on the platform Copernicus (https://cds.climate.copernicus.eu/), accessed on 24 January 2022. This data set is a combination of real measurements and model values of many climate parameters on the global scale, with a temporal resolution of one hour and a spatial resolution of 9×9 km. We downloaded the temperature and dew point at 2 m at the time of recording, atmospheric pressure at the time of recording, and precipitations (at the time of recording and daily sum). Using the Magnus equation (Magnus 1844), we calculated the relative humidity from dew point temperature and dry bulb temperature. We used the daily sum of precipitation to calculate a binary variable defining whether or not it rained on a given day (rain: >1 mm, no rain: <1 mm).

Cross-sectional study in Southern Bavaria

We monitored Chaffinches at least three times a week across one complete breeding season (15 February–22 July 2022) in Southern Bavaria, Germany. We visited forests and parks using bicycles on reduced speed or on foot. We started each survey between 11:00 and 12:00 (because rain calls were reported to be most frequent around midday (Skiba 2005)) and moved along paths in no particular order, but without passing the same path twice. Surveys lasted 60 min from the moment the first Chaffinch was heard, and we kept moving along the paths after each data point was collected. Each time a Chaffinch was heard, we localized it, noted the vocalisation type (rain call or song), time relative to solar noon, date, latitude and longitude, whether another male was countersinging (yes/no), and whether a female was spotted nearby (yes/no). In addition, we measured the ambient temperature, relative humidity, and atmospheric pressure with a portable weather station (Kestrel 4000, Nielsen-Kellermann, Boothwyn, PA, USA). We also estimated the cloud cover on a scale from 0 (0–20%) to 4 (80–100%), wind force using the Beaufort scale, and noted if it was raining (yes/no). Since, we based our analysis on the hypothesis that Chaffinches choose between rain calls and songs, birds that alternated rain calls and song were discarded, unless the bird switched vocalisation only once or twice, in which case we wrote down the vocalisation type at the first encounter. We did not record birds located less than 100 m from a previously recorded bird and sampled a different location every day to avoid accidently re–measuring the same individuals (the territory size of Chaffinches is typically around 0.7 ha, that is a circle with a diameter of about 95 m, (Skorupski et al. 2018). We complemented the weather data with measurements of the daily sum of precipitation from the closest weather station (Andechs, DWD Climate Data Center (CDC), https://cdc.dwd.de/portal/, accessed on 14 September 2022).

Longitudinal study in Bavaria

We used automatic loggers to record wild Chaffinches in gardens and forests in the wider surroundings of Augsburg and Starnberg between February and July 2022. At each location, we deployed a programmable autonomous recorder (AudioMoth Version 1.1.0, www.openacousticdevices.info) to record bird vocalisations and a weather logger (Voltcraft DL-220THP, Conrad Electronic SE, Hirschau, Germany) to measure ambient weather conditions. Since the vocal activity of birds varies throughout the day, the AudioMoths were programmed to record two 2-min files in the morning (30 and 60 minutes after sunrise), two around midday (30 minutes before and 30 minutes after solar noon) and two in the evening (30 and 60 minutes before sunset, see Supplement for details of AudioMoth programming) for two weeks, after which the recorder was relocated to record another Chaffinch territory. Chaffinches can rain–call up to 70 times per minute for several tens of minutes, hence recording the soundscape for only two minutes at a time was deemed enough to detect Chaffinch vocal activity. The sample rate of the recording was set to 32 kHz and the gain to "medium". To avoid recording human conversations, we used a high-pass filter (2 kHz) directly on the AudioMoth. Weather loggers recorded temperature, humidity, and air pressure every ten minutes. They were placed in the shade to lower the skew of temperature caused by direct sunlight exposure. Since direct sunlight on the weather loggers resulted in temperature measurement artefacts (see Supplements), we complemented the weather data using official temperature measurements (DWD Climate Data Center (CDC), accessed on 14 September 2022) from the closest weather stations (Augsburg and Wielenbach, Fig. 1c). When the difference between the temperature recorded with the weather logger and the value from the weather station was 5 °C or higher ($N=360$

of 4102), we used the measurement from the weather station instead (see Supplement for details).

We listened to the audio recordings and noted the presence of Chaffinch rain calls (0/1) and Chaffinch songs (0/1), and the presence of rain during the recording (sounds of droplets, 0/1). We also estimated the minimum number of Chaffinches vocalising on the recording (overlapping songs/rain calls or vocalisations at markedly different amplitudes). An oscillogram and a spectrogram (FFT length: 256, threshold: 0) were displayed in Avisoft SASLab Lite v. 5.3.01 for visual support.

Data analyses and statistics

Selecting all rain call recordings from Xeno-Canto, pairing them with the same number of song recordings, and excluding recordings with missing information on latitude or the recording time yielded in a total of 242 data points, 164 of them on rainy days. The temperature at the time of recording ranged from -0.6 to 34.4 °C and relative humidity from 24.4 to 97.3%. In the cross-sectional study, we observed 509 vocalising Chaffinches. We detected 116 rain-calling birds and 393 singing birds over the 79 sampling days. Rain was noted on 40 days, during which 51 birds were observed. The temperature during field observation ranged from -6.3 to 31.6 °C, the relative humidity from 31.8 to 92%. In the longitudinal study, we recorded 49 birds, totalling 4102 two-minute audio files, 1505 of which contained songs and 405 contained rain calls. We detected rain on 170 files with Chaffinch vocalisations. The temperature during our recordings ranged from -6.4 to 36.6 °C and the relative humidity from 8.2 to 100%. All statistics were performed in R v. 4.0.4. Because atmospheric pressure varies with the altitude, we accounted for the altitude–dependent variation by calculating the difference in altitude between the GPS coordinates of every sample location and Starnberg (ca. 600 m above sea level). For this, we used the package *rgbif* v. 3.7.7 and the *GeoNames* web service (https://www.geonames.org/). To normalize the measured atmospheric pressure, we multiplied the difference in altitude in meters by 0.12 (atmospheric pressure increases by about 0.12 hPa every meter (Portland State Aerospace Society 2004)) and added it to the measured value. Potential links between the weather and the probability that Chaffinches emit rain calls instead of songs were investigated with Generalized Linear Mixed Models (GLMMs) of the binomial family. We used the type of vocalisation as a binomial response variable (rain call = 1, song = 0), and weather parameters as predictor variables. A summary of the variables included in each model can be found in Table 1. In addition to weather variables, we included the hour of the observation to account for potential daily patterns in rain call emission (Bergmann 1993; Skiba 2005; Budka et al. 2019) and the day length to account for potential seasonal patterns. In the longitudinal and cross-sectional dataset, we also included the social context of vocalisations, as this probably influences vocal behaviour, as well as the observer identity to account for potential observer bias.

Finally, since the number of vocalising conspecifics may influence if a given Chaffinch sings or rain–calls, we used the longitudinal dataset to investigate the probability that rain calls are produced as a function of the number of vocalising males. We organized our dataset in the long format (two lines per recording, one for song presence and one for rain call presence) and fitted a logistic regression with the presence or absence of a vocalization as response variable, vocalisation type, number of birds and their interaction, location and time of day as fixed predictors and the recording session as random predictor.

All models were run in a Bayesian framework in R with the package *rstanarm* v. 2.21.3 with 4 chains of 5000 iterations each, a warmup of 1000 iterations, and a thinning rate of 4. We used the default, weakly informative priors (Gabry and Goodrich 2020). Furthermore, using the package *bayesplot* v. 1.10.0 and following the instructions in the associated vignettes (Gabry 2022), we checked that all chains converged well, that there was no autocorrelation between each draw, and that posterior predictive checks indicated a good model fit. Models return a posterior probability distribution for the occurrence of rain calls in relation to songs given the value of each predictor. We calculate the mean, 0.025 and 0.975 percentiles of model posterior distributions predictor estimate and 95% credible intervals.

Results

In all three analyses, the occurrence of rain calls instead of songs was not related to the presence of rain at the time of recording (Fig. 2). While a slight positive trend of an increased rain–call probability over songs during rainfall was detected in the longitudinal dataset (β_{Rain} (95% CrI) = 0.24 (– 0.20, 0.67), Table 1), the wide credible intervals illustrate the high uncertainty of this estimate. In all three analyses, the probability of rain calls over songs decreased (longitudinal study) or tended to decrease (cross sectional and European study) with temperature (Table 1). Relative humidity, atmospheric pressure, and precipitation did not correlate with the occurrence of rain calls instead of songs. Increased wind force (Fig. 2g) and cloud cover (Fig. 2h) correlated with an increased rain–call probability over songs.

The probability of rain calls in relation to songs increased over the day in all models (Fig. 3a, b), but the effect of day length (a proxy for season) was different in all three analyses (all of which had large credible intervals overlapping with 0). Rain calls were first detected two to

Table 1 Results (estimates and 95% credible intervals (CrI)) of the logistic regressions (binomial GLMM) for each of our approaches to investigate the probability of rain–call production in relation to weather conditions, temporal, and social context

	European study		Cross-sectional study		Longitudinal study	
	Predictor	Estimate (95% CrI)	Predictor	Estimate (95% CrI)	Predictor	Estimate (95% CrI)
	(Intercept)	0.1 (− 1.24, 1.5)	**(Intercept)**	**− 1.85 (−2.78, − 0.98)**	**(Intercept)**	**− 1.01 (− 1.6, − 0.43)**
Weather parameters	Rain (more than 1 mm in the day)	− 0.06 (− 0.7, 0.61)	Rain (yes)	0.11 (−0.77, 0.98)	Rain (yes)	0.25 (− 0.15, 0.69)
	Temperature (5 °C steps)	− 0.3 (−0 .62, 0.01)	Temperature (5 °C steps)	− 0.26 (− 0.65, 0.11)	**Temperature (5 °C steps)**	**− 0.19 (− 0.37, − 0.02)**
	Relative humidity (20% steps)	0.17 (− 0.23, 0.59)	Relative humidity (20% steps)	− 0.22 (− 0.81, 0.37)	Relative humidity (20% steps)	0.08 (− 0.09, 0.26)
	Corrected air pressure (10-hPa steps)	− 0.02 (− 0.09, 0.04)	Corrected air pressure (10−hPa steps)	0.18 (− 0.23, 0.6)	Corrected air pressure (10-hPa steps)	− 0.06 (− 0.26, 0.15)
	Daily sum of precipitations (mm)	− 0.02 (− 0.14, 0.11)	Daily sum of precipitations (mm)	0.04 (− 0.13, 0.22)		
			Cloud cover	**0.27 (0.04, 0.52)**		
			Wind (beaufort)	0.26 (−0.03, 0.54)		
Season/time of day	Day duration (hours)	– 0.15 (− 0.48, 0.17)	Day duration (hours)	0.30 (−0.01, 0.62)	Day duration (hours)	0.14 (− 0.16, 0.46)
	Time after sunrise (hour)	0.05 (− 0.01, 0.12)	**Time after sunrise (hour)**	**0.24 (0, 0.48)**	**Time (morning)**	**− 1.05 (− 1.47, − 0.6)**
					Time (evening)	− 0.05 (-0.41, 0.31)
Social context			Female nearby (yes)	2.71 (1.92, 3.49)		
			Countersinging male (yes)	− 0.70 (− 1.21, − 0.20)		
Location	Latitude (10° steps)	− 0.52 (− 1.36, 0.32)			Location (Augsburg)	− 1.20 (− 2.83, 0.4)
Observers					Observer 2	0.03 (− 1.04, 1.17)
					Observer 3	0.95 (− 0.59, 2.52)

The European study compared the occurrence of recordings containing rain calls to those containing songs according to the weather conditions in the database Xeno-Canto. The cross-sectional study quantified the occurrence of rain calls as opposed to songs between 11:00 and 13:00 h according to the weather conditions. The longitudinal study investigated the occurrence of rain calls among recordings of individual chaffinch activity over two weeks, according to the weather conditions. Predictors whose credible intervals did not overlap with zero are presented in bold

five weeks after the first songs (Fig. 3c, d). In the cross-sectional analysis, the probability of rain calls instead of songs increased with longer days, whereas it decreased in the Europe–wide analysis, and no effect was detected in the longitudinal analysis (Fig. 3e–g). Since the first rain calls occurred several weeks after the first song in the cross–sectional analysis, we removed the data from the first month ($N = 43$) to exclude a potentially strong leverage effect of the period without any rain calls. This sensitivity analysis showed that there was actually no effect of the day length on the rain-call-to-song ratio once the birds had started rain calling ($\beta_{\text{day length}}$ (95% CrI) = 0.13 (− 0.23, 0.49)).

In contrast to the weak weather effects, the social context strongly affected the occurrence probability of rain calls over songs. The number of vocalising males in the recordings of the longitudinal study ranged from one (1257 recordings) to four (1 recording). With increasing numbers of vocalising males, birds were more likely to produce both rain calls and songs. However, this increase was more pronounced in songs than rain calls, suggesting that birds sing more often than they rain–call when there are other males within hearing range (Fig. 4 c, ß $_{\text{Nbird: Rain call}}$ = 1.47 (0.86, 2.16), Table S1). Similarly, in the cross–sectional study, we found that the probability of rain calling decreased when a countersinging male was present (Fig. 4 a). Most interestingly, the male Chaffinches were

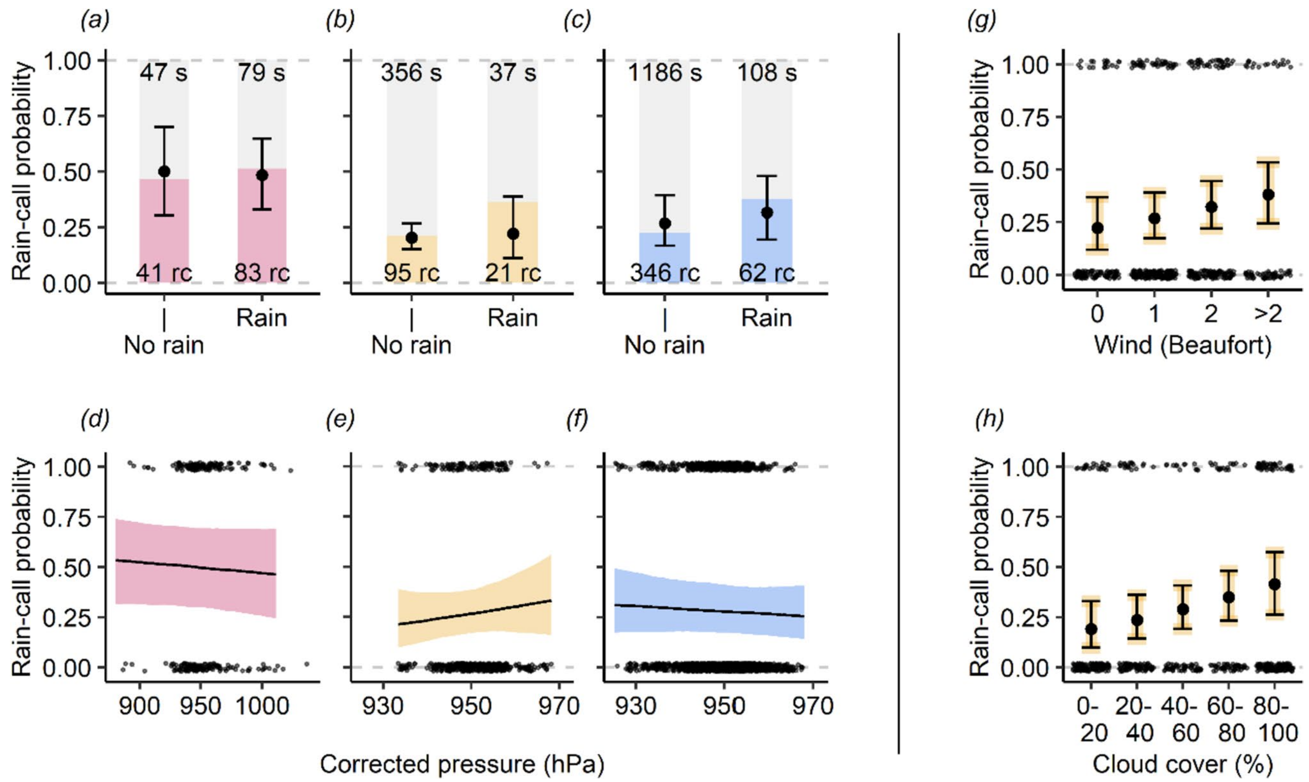

Fig. 2 The presence of rain and atmospheric pressure did not influence the probability of producing rain calls instead of songs, but rain calls were used more often in windy and cloudy conditions. Analyses are color coded: Estimates coming from the European study are depicted in red, results of the cross-sectional study in yellow and results from the longitudinal study in blue. **a–c** model estimate and 95% credible interval of the effect of the presence of rain during the recording for the European study (**a**), at the moment of observation for the cross-sectional analysis (**b**) and on the recording for the longitudinal analysis (**c**). The proportion of rain calls (colour bar) and songs (grey bar) is shown in the bar plot, the sample size is written on each bar (rc = rain calls, s = songs); **d–f** effect (model estimate and 95% credible interval) of the atmospheric pressure on the probability to hear rain calls instead of songs **d** in the European analysis, **e** the cross-sectional analysis and **f** in the longitudinal analysis. Atmospheric pressure was corrected for altitude-dependent variations. Data points are shown in black (points on the 0-line represent songs, points on the 1-line rain calls); **g** high wind increase the probability of hearing rain calls instead of songs. Estimate and 95% credible intervals for the wind force on the Beaufort scale in the cross-sectional analysis. **h** cloud cover increases the probability of hearing rain calls instead of songs in the field observation model. Estimate and 95% credible interval of the cloud cover in the cross-sectional analysis

much more likely to produce rain calls instead of songs when a female was close by (Fig. 4 b).

Discussion

In this study, we investigated the long–standing hypothesis that Chaffinches choose to rain call rather than to sing in adverse weather conditions. For this, we used three independent approaches: analysis of recordings from the Xeno-Canto database, opportunistic observations in the field, and longer systematic monitoring of Chaffinches at given locations. We then used logistic GLMMs to investigate whether Chaffinches substitute songs for rain calls in relation to the weather conditions. In none of the three approaches did we find strong statistical support for an association between rainy weather and the occurrence of rain calls (but rain calls were more frequent in colder and cloudy conditions). Instead, we found that the occurrence of rain calls varied considerably with the social context: males preferably rain–called when a female was close by and less often when another, or several other, males were vocalising too.

We found no correlation between the occurrence of rain calls and songs and rainfall in any of our three studies, and minor effects of other parameters compared to that of the social context. Therefore, we are confident to conclude that Chaffinches do not trade–off songs for rain calls based on the ambient weather conditions. That Chaffinches do not predict rain, or do not change their vocal behaviour in relation to rainfall, is in line with the results reported by three of the six previous studies investigating the effect of weather on rain-calling behaviour (Groebbels 1957; Voigt and Bezzel 1961; Skiba 2005). After all, this lack of an effect is not surprising. On the contrary, it would have been difficult to explain

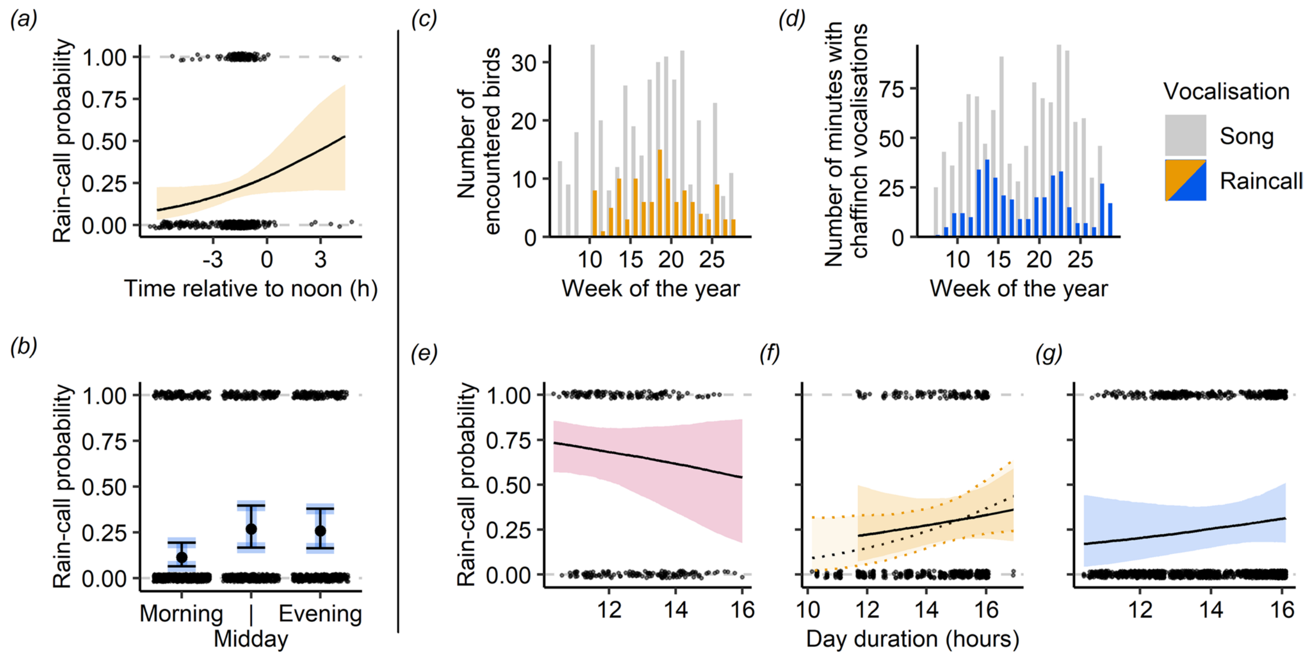

Fig. 3 Time of day influenced the occurrence of rain calls instead of songs in the cross-sectional dataset (**a**) and in the longitudinal dataset (**b**) and rain calling started later in the season than song (**c–d**) but the season had no consistent effect across models (**e–g**). The analyses are color coded (European study in red, cross-sectional in yellow, longitudinal study in blue). Estimates and credible intervals for the effect of the time of recording relative to noon in the cross-sectional data (**a**) and of the time of recording in the longitudinal data (**b**). Number of birds (**c**) or of recordings (**d**) that presented rain calls (colored) and songs (grey) across the season in the cross-sectional **c** and longitudinal (**d**) dataset. Estimates and 95% credible intervals of the effect of day duration in the European data (**e**), the cross-sectional data (**f**) and the longitudinal data (**g**). Raw data points are shown in black (points on the 0-line represent songs, points on the 1-line are rain calls). In the cross-sectional data, the results of the model including all data points are shown with dotted lines while the results of the sensitivity analysis, including only vocalisations after the first rain call was heard, are shown with a solid line

why Chaffinches would use a call to indicate rain or why they switch vocalisation types when the weather changes. While it is well known that birds decrease vocal activity in bad weather conditions (Lengagne and Slater 2002; Bruni et al. 2014), changes in call type according to the weather have not been observed yet. Previous observations that Chaffinches did indeed increase the frequency of rain calls in rainy conditions (Heyder 1954; Jakobs 1963; Kemme 1983) could be due to several artefacts related to low sample sizes or observer-expectancy bias, or both.

We found that Chaffinches produced more rain calls in relation to songs at lower temperature, increasing wind and cloud cover, similar to what Skiba (2005) described. Why the birds would use more rain calls than songs in cold or windy conditions is yet unclear. In bad weather conditions, signal transmission is disrupted (Lengagne and Slater 2002) and rain calls might propagate better than songs in poor acoustic conditions because of their simpler structure. Alternatively, our result could also reflect a decrease in singing activity and no change in rain-calling activity. However, it is important to note that the observed weather effects were quite small (estimate 0.2) while rain-calling behaviour varied chiefly with the social context (estimate 2.5). Thus, we may conclude that social functions, and not weather conditions, are predominant for male Chaffinches in deciding whether to sing or to rain–call. In this sense, it is quite possible that the weak cloud-cover/wind effect is an indirect one that is driven by the social context, in as much as more cloud cover and higher wind speeds might cause the female to keep a closer distance to the male and, as a consequence, the male is more likely to rain–call because of the female presence.

Regarding the day duration, our three studies yielded conflicting results: in the European data set rain–call probability decreased with increasing day length, while the longitudinal and the cross–sectional analysis showed no meaningful relation between the day length and rain–call probability. If rain calls have a similar function to songs, as suggested by (Bergman 1953), one would expect a parallel increase of rain call and song emission across the breeding season and thus a stable rain-call-to-song ratio, as found in the longitudinal and cross–sectional study. Maybe bias in the uploaded files to the Xeno-Canto database can account for the observed seasonal effect. Recordists might neglected rain calls later in the season as they appear less interesting than songs because of their simpler structure. This would result in a spurious decrease in rain call probability with increasing

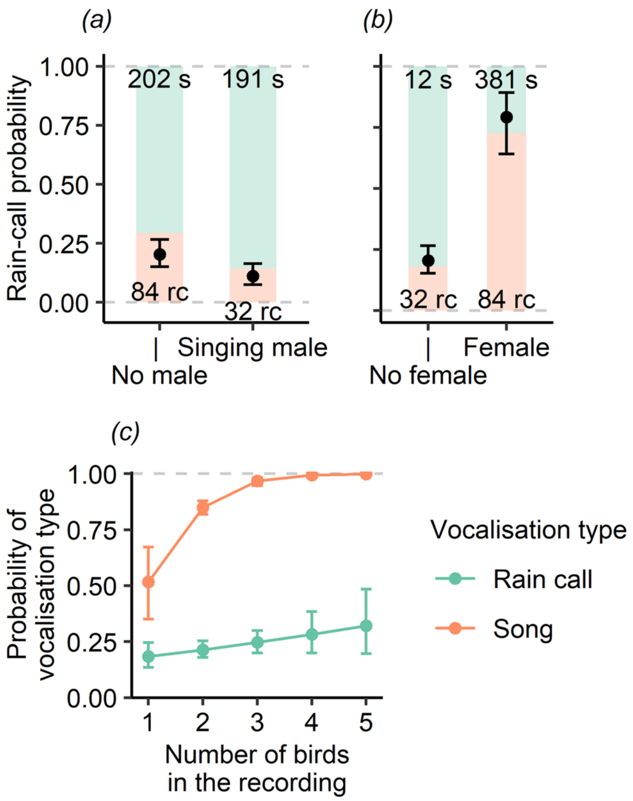

Fig. 4 The social context greatly influenced the probability of producing rain calls instead of songs. Estimates and 95% credible intervals of the rain call probability in relation to the presence of a female (**a**) or a countersinging male (**b**) in the cross-sectional analysis (rc = rain calls, s = songs). The number of vocalising males increased the probability of song and call production in focal males in the longitudinal study, but the increase in song was much stronger (**c**), estimates and 95% credible intervals

day length. Such an effect is typical for opportunistic–sampling data bases (Isaac et al. 2014; Isaac and Pocock 2015), for example, birdwatchers tend to report their first detection of migratory birds in a year and then neglect the species as it becomes more common (Dachverband Deutscher Avifaunisten 2011).

In this study, we hypothesized that rain calls are used by male Chaffinches as a substitute for songs in adverse conditions, as suggested by (Bergman 1953). In line with this notion, we never observed any rain–calling females. However, we found that rain calls and songs were used by male Chaffinches in different social contexts. Songs were produced more often with increasing numbers of other singing males within earshot, while rain calls were used three times as often when a female was present. This suggests that rain calls and songs have different functions. Rain calls might predominantly address female Chaffinches as a form of pair bonding or some other mate–directed function. This would explain why rain calls are not heard in the very beginning of the breeding season, when males are not yet paired, but further investigation is necessary to support this hypothesis. In particular, it would be interesting to conduct playback experiments on both sexes to test their reaction to rain calls.

In Chaffinch songs, males and females seem to pay attention to different parts: females are attracted by complex flourishes at the end of strophes, while long trills, which precede the flourish, are used in male-male interactions (Riebel and Slater 1998b; Leitão et al. 2006). Closely related species, such as the Tenerife Blue Chaffinch (*Fringilla teydea*) and the Gran Canaria Blue Chaffinch (*Fringilla polatzeki*), also use a song and a rain call with very similar structures (Bergmann et al. 2008). Interestingly, the song of Bramblings (*Fringilla montifringilla*) is a long trill that resembles an extended Chaffinch rain call of the "rültsch" dialect (Marler 1956; Haftorn 1993). Some other related species, such as the European Greenfinch (*Chloris chloris*) also have a two–part song with a more complex trill and a simpler call–like part ("chirr"), which can be emitted together or independently (Bergmann et al. 2008). Although a change in the rain–calling activity was detected in the context of territory intrusion (Budka et al. 2019), it would be inappropriate to categorize the Chaffinch rain call as a song, since it is also used in predator mobbing (at high rates and interspersed with the typical mobbing "chink" call (Marler 1956; von Haartman and von Numers 1992; Bergmann 1993)). Perhaps the rain call is used to attract the mate in a mobbing situation, while the pink call is alerting her to the danger. If this is true, the combinatorial signal sequence would resemble monkey call syntax (Arnold and Zuberbühler 2006) or the mobbing call system of tits (Suzuki et al. 2016).

Conclusions

The present study shows that the rain call of Chaffinches is not triggered by rainfall as previously suggested. Instead, male Chaffinches appear to direct their calls at females, as indicated by the increased frequency of rain calls in the presence of females. To further elucidate the function of the rain call, it would be interesting to investigate a possible link to courtship or breeding behaviours, e.g., through playback experiments and behavioural observations, and we are continuing our studies in this direction. The rain call is just one example of the various calls of birds, and our study also makes a case for the need to improve our understanding of bird calls in general. Unlike songs, calls are given by almost all bird species and in all seasons. Yet, our knowledge of calls is far more limited than that of songs. We hope that this study encourages more researchers to investigate the role of calls for bird behaviour.

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Data availability Data and code are available from the Zenodo research repository (https://doi.org/https://doi.org/10.5281/zenodo.10513369).

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