Do Weather Conditions during the Brood Rearing Period Affect the Survival of Owl Chicks on a Subtropical Island?

Authors: Kanasugi, Naoki, Sawada, Akira, Nakamura, Haruka, Kumagai, Shun, Ono, Haruka, et al.

Source: Ornithological Science, 23(2) : 65-76

Published By: The Ornithological Society of Japan

URL: https://doi.org/10.2326/osj.23.65

Ornithol Sci 23: 65–76 (2024)

ORIGINAL ARTICLE

Do weather conditions during the brood rearing period affect the survival of owl chicks on a subtropical island?

Naoki KANASUGI[1,*], Akira SAWADA[2], Haruka NAKAMURA[1], Shun KUMAGAI[1], Haruka ONO[1], Mari ESASHI[1], Shuya NAGAI[1], Ryota MURAKAMI[4], So SHIRAIWA[1], Tetsuya IWASAKI[3] and Masaoki TAKAGI[1,#]

[1] *Department of Natural History Science, Graduate School of Science, Hokkaido University, Kita 10, Nishi 8, Kita-ku, Sapporo 060–0810, Japan*
[2] *Biodiversity Division, National Institute for Environmental Studies, Ibaraki 305–8506, Japan*
[3] *Department of Biology and Geosciences, Graduate School of Science, Osaka City University, Osaka 558–8585, Japan*
[4] *Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa 277–8564, Japan*

ORNITHOLOGICAL SCIENCE

Abstract Suitable climatic conditions for the species are known to improve the breeding success of birds, and the ways in which climatic conditions affect bird breeding have been well studied in temperate and subarctic zones. However, hypotheses made from limited regional information may not be adaptable to other regions, and studies in other areas are needed. It is important to determine the impact of weather conditions on birds on isolated islands, because it is difficult for them to adjust their habitats in response to climate conditions. This study elucidated the effects of weather conditions on the breeding of Ryukyu Scops Owls *Otus elegans* on the subtropical Minami-daito Island, Japan. The study used data from 806 chicks over a six-year period from 2016 to 2021. We found that heavy rain caused increased chick mortality. Chicks weighed less and had shorter tarsi and wings when precipitation was higher. Structural equation analysis showed that high precipitation reduced chick weight and indirectly increased mortality. Heavy rains were thought to have restricted the foraging behaviour of the parents, resulting in a decrease in chick weight.

Key words Breeding, Climate change, *Otus elegans*, Precipitation, Subtropical

The effects of climate change have been noted in many species, and are becoming better understood (Scheffers et al. 2016). It is important to assess climatic factors that affect the breeding of birds to predict the effect of long-term climate change on the population. Most previous studies have been conducted in temperate and subarctic zones (Feeley et al. 2017). Hypotheses made from limited regional information may not be adaptable to other regions (Gordo & Doi 2012; Charmantier & Gienapp 2014; Hidalgo Aranzamendi et al. 2019). Consequently, studies from regions other than temperate and subarctic zones are needed to assess global impacts better.

Species living at low latitudes, where seasonal changes are minimal, have adapted to a limited range of climatic conditions, making them potentially more vulnerable to climate change effects (Deutsch et al. 2008; Sheldon et al. 2018). In fact, few studies on the impacts of climate change on birds at low latitudes show that birds shift to a higher elevation with increased temperature (Freeman & Class Freeman 2014; Freeman et al. 2018; Bender et al. 2019; Neate-Clegg et al. 2021). This is probably because climate change has made the climatic conditions of their original habitat unsuitable for breeding. Additionally, for species that inhabit small, isolated islands with little variation in climate factors, it is difficult for them to change habitats even when weather conditions are no longer suitable. From this perspective, it is an immediate priority issue to study species in

(Received 4 January 2023; Accepted 22 January 2024)
Corresponding author, E-mail: mtakagi@eis.hokudai.ac.jp
* Present address: *Department of Natural History Science, Graduate School of Science, Hokkaido University, Kita 10, Nishi 8, Kita-ku, Sapporo 060–0810, Japan*

a geographically isolated habitat at lower latitudes (Shiao et al. 2015, 2020; Taylor et al. 2021).

Understanding the specific mechanisms behind these weather condition impacts, e.g. high or low temperatures, heavy rainfall, drought, or strong winds, is also crucial. However, many studies, regardless of the region, have only clarified the relationship between weather conditions and reproductive success, and there is insufficient verification of the mechanisms by which weather conditions affect reproductive success (Anctil et al. 2014). Potential mechanisms could be direct ones, such as heat stroke (Salaberria et al. 2014; Rodríguez & Barba 2016) and hypothermia (Anctil et al. 2014), or indirect such as starvation due to infrequent parental feeding and a resulting slowing of growth rates (Winkler et al. 2013). We speculated that by considering the relationship between chick survival, chick growth and weather, it would be possible to clarify which weather factors influence the fate of chicks and through which mechanisms. We chose structural equation models (SEM) to perform this analysis. By using SEM, the direction of causality can be tested directly. Furthermore, using a variable as both a response in one path and as a predictor in another, we can also test indirect effects which cannot be represented by any single model (Lefcheck 2016).

To investigate the impact of weather on chicks and its mechanisms on non-temperate and non-subarctic islands, this study investigated how weather conditions affect the breeding of Ryukyu Scops Owl *Otus elegans interpositus* on Minami-daito Island, Japan (25°50′47″N,131°13′23″E). Minami-daito Island is an isolated oceanic island in the subtropical climate zone. It is a small island with little variation in environmental factors such as elevation, land-use and climate. In this study, we determined which weather conditions affect the growth and mortality of chicks. Furthermore, we examined whether mortality is caused directly or indirectly by the weather conditions.

MATERIALS AND METHODS

1) Study species

The Ryukyu Scops Owl lives on small islands, ranging from Okinoshima in Kyushu, Japan, to Babuyan Islands in the Philippines (Takagi et al. 2015; Gill et al. 2023). Minami-daito Island, the location of this study, is geographically distant from other islands and the owl population on this island is known to be genetically isolated, with little genetic exchange (Masaoki Takagi & Takema Saito unpublished data). This population is considered to be of an endemic subspecies, Daito Scops Owl *O. e. interpositus*, and is listed as endangered (Ministry of the Environment 2020). The owls nest in natural tree cavities and nest boxes we set up to raise their chicks (Takagi et al. 2007). Egg laying takes place from mid-March to mid-May, and clutches range in size from one to four eggs (Takagi et al. 2007; Akatani et al. 2011; Sawada unpublished data). Feral Cat *Felis catus* and Japanese Weasel *Mustela itatsi*, which were introduced by humans, inhabit the island, and sometimes prey on owl chicks (Takagi et al. 2007; Akatani & Takagi 2020).

2) Study area

We studied a population of Ryukyu Scops Owl on Minami-daito Island, Okinawa prefecture, Japan. The island is small and flat (30.57 km², highest elevation 75 m), situated approximately 360 km east of Okinawa Island, the next nearest island in the range of the species. The population on Kita-daito Island, an island only 8 km away from Minami-daito Island, is known to have become extinct (Anezak 2012). Minami-daito Island features a subtropical climate, with an annual average temperature of 23.5°C and an annual average precipitation of 1,639 mm between 1991 to 2020 (Japan Meteorological Agency 2021). The heaviest precipitation of the year is in May (Japan Meteorological Agency 2021), which often coincides with the brood-rearing period. Most of the island is covered with sugar cane fields and the owls inhabit the windbreak forest around the crop fields. The windbreak forest is composed of Chinese Fan Palm *Levison chinensis var. amanoi*, Casuarina *Casuarina spp*., Chinese Banyan *Ficus acrocarpa* and Lead Tree *Leucaena lencocephala*. The owls nest in natural cavities in Chinese Fan Palm or Casuarina, or in the 170 nest boxes set up around the island.

3) Data collection

Nest monitoring

We studied the survival of chicks from hatching to fledging, from 2016 to 2021. From late February to late May, we determined the clutch initiation date by inspecting nest boxes and natural nests for the presence of eggs, every two to four days. The incubation period of Ryukyu Scops Owl is about 26 days (Takagi et al. 2007). Consequently, we monitored nest boxes daily, beginning 26 days after clutch initiation, to determine the hatching date of the first chick. If that date could not be determined, the chicks were weighed when discovered and the date was estimated using a growth curve (Sawada et al. 2021).

Survival data

Knowing that chicks typically leave the nest around 25 days old, with the hatch date considered as day 0, we checked the nests daily from day 25 onward to count the number of chicks that had successfully fledged. The number of dead chicks was recorded if a dead body was found in the nest box between predicted hatching and fledging dates. If signs of an attack were observed, such as scattered feathers in the nest, we attributed the death to predation.

Morphometric data

Morphometric measurements of chicks were taken at 20 days of age. We measured weight, tarsus length, and wing length. Weight was recorded to the nearest 0.1 g using an electronic scale. Tarsus length was measured to the nearest 0.01 mm using a digital caliper. Wing length was measured to the nearest 0.5 mm by lightly pressing the wing against a ruler. We measured tarsus and wing length twice, and the average value was used for analysis. These morphometric measurements were performed by the same investigator.

Meteorological data

Climate data from 2016 to 2021, recorded at Minamidaito Meteorological Station (25°49′7″N, 131°13′7″E, 15 m) by the Japan Meteorological Agency (JMA), were utilized for this study (Japan Meteorological Agency 2021). We used three weather condition parameters: temperature, precipitation and wind speed. Specifically, we used 'daily temperature', 'cumulative daily precipitation' and 'average daily wind speed' as our data points.

4) Data analysis

Description of the effect on reproductive output

The impact of weather conditions on chick survival was analysed using a generalized linear mixed model (GLMM). This model included binary variables for chick survival (death: 1, survival: 0) as response variable, with weather condition parameters (temperature, precipitation, and wind speed) and nest type (natural nest: $n=64$ or nest box: $n=742$) as the explanatory variable, and each clutch ID and year as random effects. The chicks identified between 2016 and 2021, excluding those killed by predation, were used in the analysis. The data set included 806 individuals, of which 135 chicks died before fledging. Because the earliest chick left the nest at about 25 days old, the weather parameters were as follows: for temperature, the cumulative average temperature from 0 to 25 days of age; for precipitation, the cumulative daily precipitation from 0 to 25 days of age; and for wind speed, the cumulative average wind speed from 0 to 25 days of age; all variables were standardised. All explanatory variables were tested for multicollinearity using R package 'car' (Fox & Weisberg 2019) and were not correlated with each other (all $VIF<3.0$, Table S2). We performed GLMM using R package 'lme4' (Bates et al. 2015), using a binomial distribution for the error distribution and 'logit' for the link function. Model selection was performed by determining the AIC for all variable combinations. Models with a difference of less than two from the minimum AIC were averaged using the 'MuMIN' package (Bartoń 2020).

Mechanism of the effect on reproductive output

We examined the effect of weather conditions on chick growth using GLMM with morphometric measurements (weight, tarsus length, and wing length) of chicks at 20 days of age as response variables, weather condition parameters, hatching order and nest type (natural nest: $n=44$ or nest box: $n=650$) as explanatory variables, and each clutch ID and year as random effects. A total of 694 individuals whose body weight, tarsus length, and wing length were measured at 20 days of age from 2016 to 2021, were included in the analysis. The weather parameters were as previously described, except the accumulation was taken between 0 to 19 days of age. Owls start incubating before the entire clutch is complete, resulting in a common occurrence of asynchronous hatching (Iwasaki unpublished data). We could estimate hatch order from the order of body mass because weight gain had not yet reached the upper limit at the time of measurement (Sawada et al. 2021). The hatching order was determined by considering the order to correspond to the chick weight at 20 days of age, with the first hatching chick as '1'. If two chicks weighed the same, they were given the same hatching number. All explanatory variables were tested for multicollinearity using R package 'car' and were not correlated with each other (all $VIF<3.0$, Table S2). We performed GLMM, using a gamma distribution for the error distribution and 'log' for the link function. Model selection was performed with the same method described above.

To investigate the relationship between chick survival, chick growth and weather, SEM was performed to determine whether chick mortality was due to direct or indirect climate factors. The analysis included 694 individuals measured for morphometric traits (weight, tarsus length, and wing length) at 20 days old, from 2016 to 2021, with 68 of these chicks dying before leaving the nest. The weather parameter was the cumulative daily precipitation from 0 to 19 days of age. The hatching order was determined by considering the heaviest nestling at 20 days of age to have hatched first. The nest type included 42 chicks in natural nests and 652 chicks in nest boxes. We performed the analysis with the 'psem' function of the 'piecewiseSEM' package in R (Lefcheck 2016), which can accommodate multiple error structures. This is important because the response terms of our component models have different distributions. Since precipitation was considered to be the primary influence on chick survival and growth from the relationship between climate and morphological traits, the analysis focused on precipitation. All explanatory variables were tested for correlation. We assumed that morphological traits are correlated, because tarsus length and wing length were correlated (Tarsus length: VIF=3.200, Wing length: VIF=3.054). None of the other variables showed any correlation with each other (all VIF<3). We made the following three hypotheses: (1) Chick survival is influenced by morphological traits (weight, tarsus length, and wing length at 20 days of age), precipitation prior to measurement, and nest type, as estimated by a Generalized Linear Mixed Model (GLMM) with a binomial error structure and a 'log' link function, considering clutch ID and year as random effects. (2) Chick body mass is likely influenced by the precipitation before measurement, hatch order and nest type. Additionally, tarsus length and wing length are expected to be affected by the precipitation before measurement and hatch order. These factors were considered the primary influencers of growth, as determined by GLMM with a gamma error structure and a 'log' for the link function, incorporating clutch ID and year as random effects). (3) Three morphological traits (body weight, tarsus length, and wing length) were assumed to be correlated. The adequacy of the piecewise SEM was evaluated using a Shipley's d-separation with the model considered adequately fitted if the p-value was greater than 0.05. We calculated chi-square values with the 'LLchisq' function of the 'piecewiseSEM' package in R. This value was used to calculate the RMSEA according to the formula of Kenny et al. (2015) and we considered the model to be fitted if RMSEA<0.05.

RESULTS

1) The effect of weather conditions on chick survival

From 2016 to 2021, the hatch dates of 832 chicks were recorded, of which 26 were considered to have been predated and an additional 135 individuals died from other causes. Thus, predation accounted for approximately 16% of the total 161 deaths. Overall, mortality was low, but varied between years (Fig. S1). Model selection suggested that any weather factor (precipitation, temperature, or wind speed) and nest type may affect the survival of chicks (Table 1). Precipitation, wind speed and nest type were specifically included in all selected models. The averaged model showed that the mortality rate was significantly higher with higher precipitation (Table 2, Fig. 1-A, Estimate coefficient=0.546 P=0.0267). Based on this estimate, an increase of 1 standardised precipitation value (174.90 mm during 26 days after hatching), would result in a 1.73-fold increase in mortality odds. Temperature was not significantly associated with mortality rates (Table 2, Fig. 1-B), although there was a tendency toward higher mortality with lower temperature. When wind speed increased, mortality rate significantly decreased (Table 2, Fig. 1-C, Estimate coefficient=−0.404 P=0.0353). An increase of 1 standardised value in wind speed increase (8.49 m/s during 26 days after hatching) in wind speed can cause a 0.67-fold decrease in mortality. The mortality rate in nest boxes was slightly higher than in natural

Table 1. AIC values for each model of chick mortality (ΔAIC≦2.0).

Response variable	Model	AIC	ΔAIC
Chick mortality	~Precipitation+Temperature+Wind+Nest type	662.6	0
	~Precipitation+Wind+Nest type	665.4	1.27

Table 2. Estimate of GLMM for chick mortality.

Response variable	Explanatory variable	Coefficient	P value
Chick mortality	Intercept	−3.271	0.0000
	Precipitation	0.547	0.0267
	Temperature	−0.304	0.0630
	Wind	−0.404	0.0353
	Nest type : Nest box	1.027	0.0700

nests, but not significantly so (Table 2, Fig. S2-a).

2) The effect of weather conditions on chick growth

Model selection suggests that precipitation, temperature, wind speed, hatching order and nest type may affect morphological traits of chicks (Table 3). Precipitation was included in all selected models for weight and tarsus length (Table 3). In addition, averaged models showed that when precipitation increased, chicks weighed less and had shorter tarsi and wings (Table 4, Fig. 2-a, b and c, $P<0.05$). This result suggests that an increase of 1 standardised value in precipitation (133.92 mm during 19 days after hatching) produced a 0.96-fold decrease in body weight, a 0.99-fold decrease in tarsus length and a 0.99-fold decrease in wing length. Additionally, the averaged model of wing length showed a trend towards longer wing lengths with higher temperature (Table 4, Fig. 2-f). This result suggests that an increase of 1 standardised value in temperature (26.24°C during 19 days after hatching) produced a 1.01-fold increase in wing length. The effects of wind speed were not significant. Hatching order was included in all models (Table 3). In all averaged models, the younger siblings had smaller morphometric measurements (Table 4). However, since the "hatching order" used in this study was estimated according to the weight order within the brood, this is almost an inevitable result. The effect of nest type was significant only in body mass. Chicks in nest boxes were 0.96-fold lighter than those in natural nests (Table 4, Fig. S2-b).

3) How weather conditions affect survival

The Structural Equation Modelling explained 67% of chick mortality (Fig. 3 and Table S1, Fisher's $C=0.608$ ($p=0.738$), $\chi^2=0.113$ ($p=0.737$), $RMSEA=0.00$). High precipitation before measure-

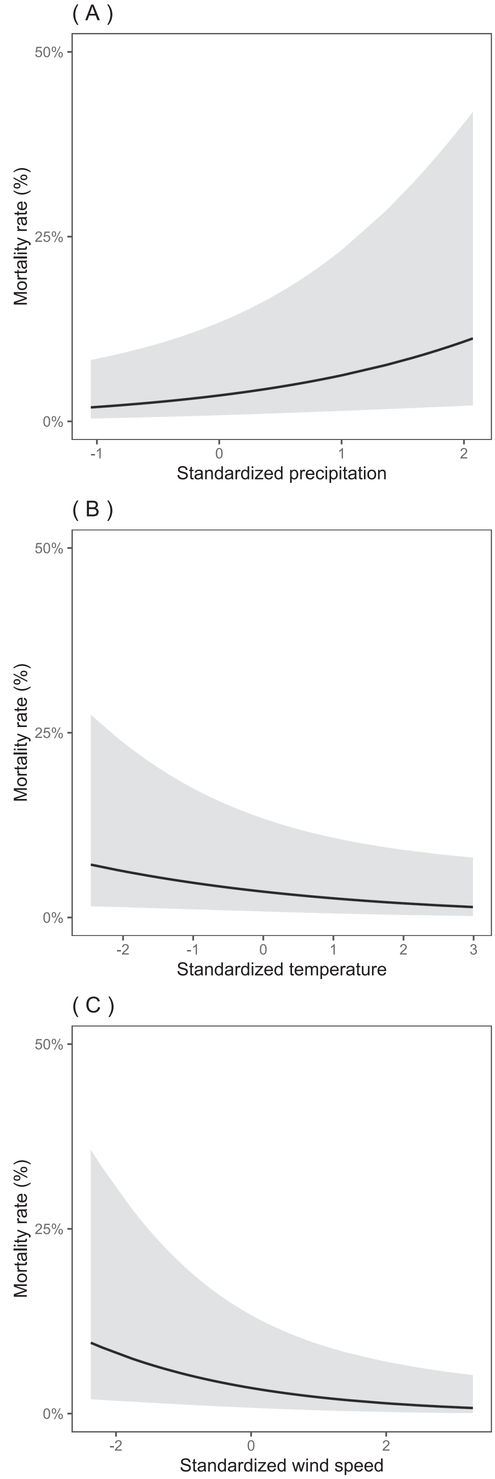

Fig. 1. The effect of weather conditions on chick mortality rate estimated by GLMM with 95% confidence intervals. (A) The effect of precipitation; The standardised precipitation of 0 is 184.79 mm. (B) The effect of temperature; The standardised temperature of 0 is 650.96. (C) The effect of wind speed; The standardised wind speed of 0 is 106.30 m/s.

Table 3. AIC values for each model of chick growth (ΔAIC≦2.0).

Response variable	Model	AIC	ΔAIC
Body mass	~Precipitation+Hatch order+Nest type	4412.2	0.00
	~Precipitation+Hatch order	4412.6	0.44
	~Precipitation+Wind+Hatch order+Nest type	4413.8	1.61
	~Precipitation+Temperature+Hatch order+Nest type	4413.9	1.69
	~Precipitation+Temperature+Hatch order	4414.1	1.89
Tarsus length	~Precipitation+Hatch order	2007.1	0.00
	~Precipitation+Temperature+Hatch order	2007.4	0.30
	~Precipitation+Wind+Hatch order	2008.2	1.17
	~Precipitation+Hatch order+Nest type	2008.6	1.52
	~Precipitation+Temperature+Hatch order+Nest type	2008.6	1.54
	~Precipitation+Temperature+Wind+Hatch order	2009.0	1.93
Wing length	~Precipitation+Temperature+Wind+Hatch order	4827.6	0.00
	~Precipitation+Temperature+Hatch order	4827.7	0.09
	~Precipitation+Temperature+Hatch order+Nest type	4827.9	0.31
	~Precipitation+Temperature+Wind+Hatch order+Nest type	4828.0	0.41
	~Temperature+Hatch order+Nest type	4828.2	0.56
	~Temperature+Hatch order	4828.2	0.57
	~Precipitation+Hatch order	4828.9	1.25
	~Temperature+Wind+Hatch order	4829.0	1.36
	~Hatch order	4829.1	1.47
	~Temperature+Wind+Hatch order+Nest type	4829.1	1.48

Table 4. Estimate of GLMM for chick growth.

Response variable	Explanatory variable	Coefficient	P value
Body mass	Intercept	4.510	<2e-16
	Precipitation	−0.039	<2e-16
	Temperature	−0.005	0.3500
	Wind	−0.005	0.3515
	Hatch order	−0.087	<2e-16
	Nest type	−0.043	0.0233
Tarsus length	Intercept	3.379	<2e-16
	Precipitation	−0.014	<2e-16
	Temperature	0.004	0.0822
	Wind	−0.002	0.2865
	Hatch order	−0.035	<2e-16
	Nest type	−0.008	0.2998
Wing length	Intercept	4.600	<2e-16
	Precipitation	−0.012	0.0254
	Temperature	0.012	0.014
	Wind	0.009	0.0975
	Hatch order	−0.101	<2e-16
	Nest type	−0.031	0.0906

ment resulted in increased mortality, primarily due to decreased body weight. Additionally, precipitation prior to measurement influenced tarsus length; however, tarsus length did not show a significant correlation with mortality. The direct relationship between precipitation and mortality was not significant. The study also found correlated errors among different morphological traits.

DISCUSSION

1) Effects of weather conditions in the subtropics

Precipitation significantly increased chick mortality and made the growth of chicks worse (details of the impact on morphology are discussed below). The effect of rainfall in the subtropical zone was more similar to that of temperate zones than arid zones. In Taiwan, which belongs to the same subtropical zone as Minami-daito Island, chick mortality increases after heavy rainfall (Shiao et al. 2015). Additionally, frequent precipitation increased chick mortality in birds in southwestern China, which has a subtropical climate (Liu et al. 2021). Not contrary to these studies, our results also showed that seasonal rainfall was

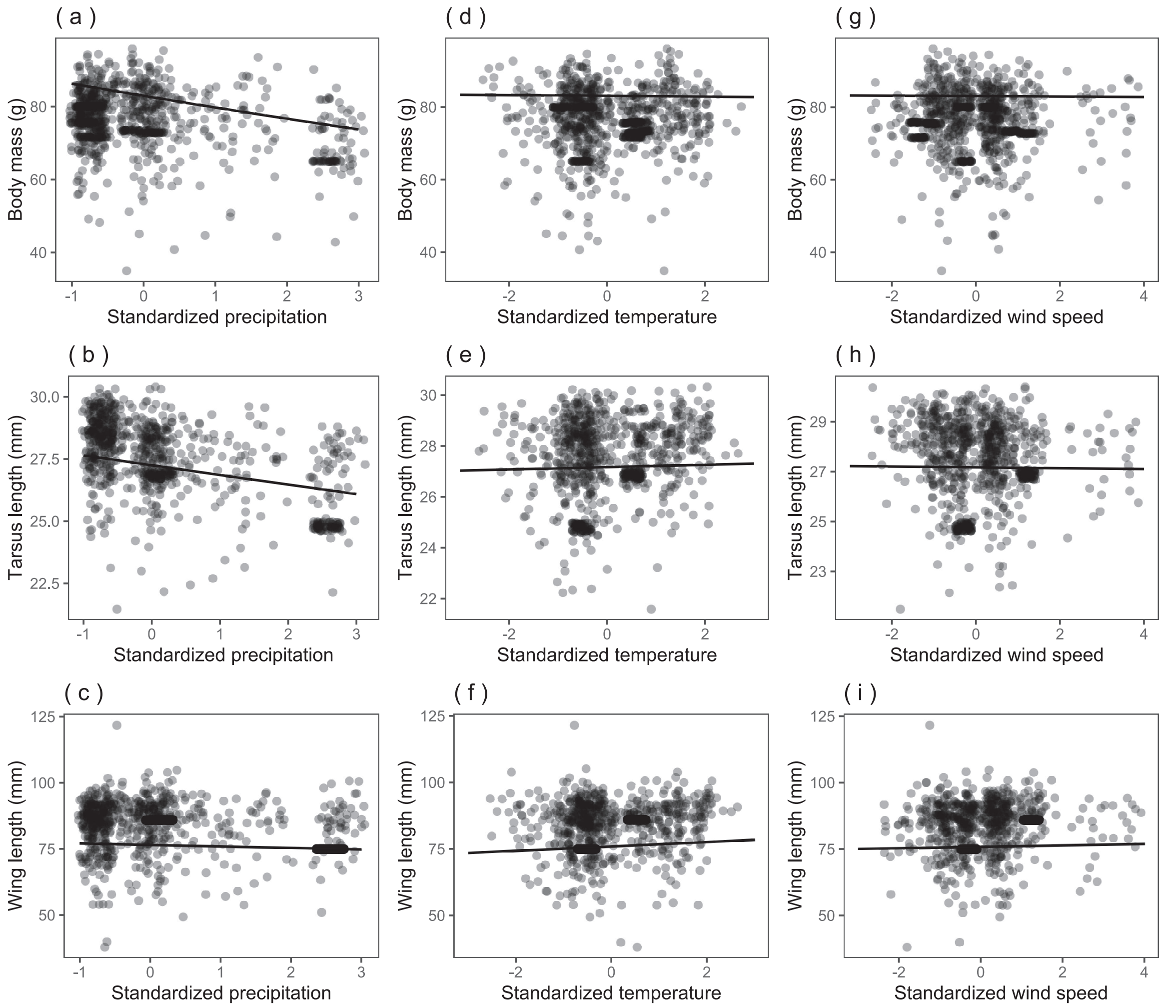

Fig. 2. The effect of weather conditions on chick morphological traits estimated by GLMM. (a.~c.) The effect of precipitation in morphological tarts; The standardised precipitation of 0 is 112.64 mm. (d.~f.) The effect of temperature in morphological tarts; The standardised temperature of 0 is 494.64°C. (g.~i.) The effect of wind speed in morphological tarts; The standardised wind speed of 0 is 81.34 m/s.

damaging, not beneficial, to subtropical owl species. In subarctic to temperate owl species, precipitation during the breeding season is also known to negatively affect chicks such as by increasing mortality (Peery et al. 2012; Fisher et al. 2015). However, it is also known that with owl species in extremely dry arid zones, high precipitation increases breeding success (Seamans et al. 2002; Peery et al. 2012; Comay et al. 2022). Consistent trends in the effects of precipitation in tropical regions are unknown due to a lack of sufficient studies, but there are some known cases of both increased and decreased mortality with high precipitation (Senapathi et al. 2011; Oppel et al. 2013; Tarwater & Beissinger 2013), and also no effect of precipitation fluctuations (Brawn et al. 2011; Styrsky & Brawn 2011). Weak rainfall may not affect nestling survival in the arid zones and the dry regions of the tropics (Chausson et al. 2014; Shiao et al. 2015). This is because the precipitation levels do not reach a harmful threshold, and the benefits, such as increased food availability due to rainfall, are more prominent (Lima et al. 2002). However, the rainfall on Minami-daito Island is likely to be sufficiently high to increase mortality. Thus, birds in the subtropical zone were thought to respond to rainfall more similarly to those in temperate zones than those in arid zones.

In our study, low temperatures tended to increase chick mortality and decrease wing growth. Similarly, in Taiwan, birds showed lower breeding success at

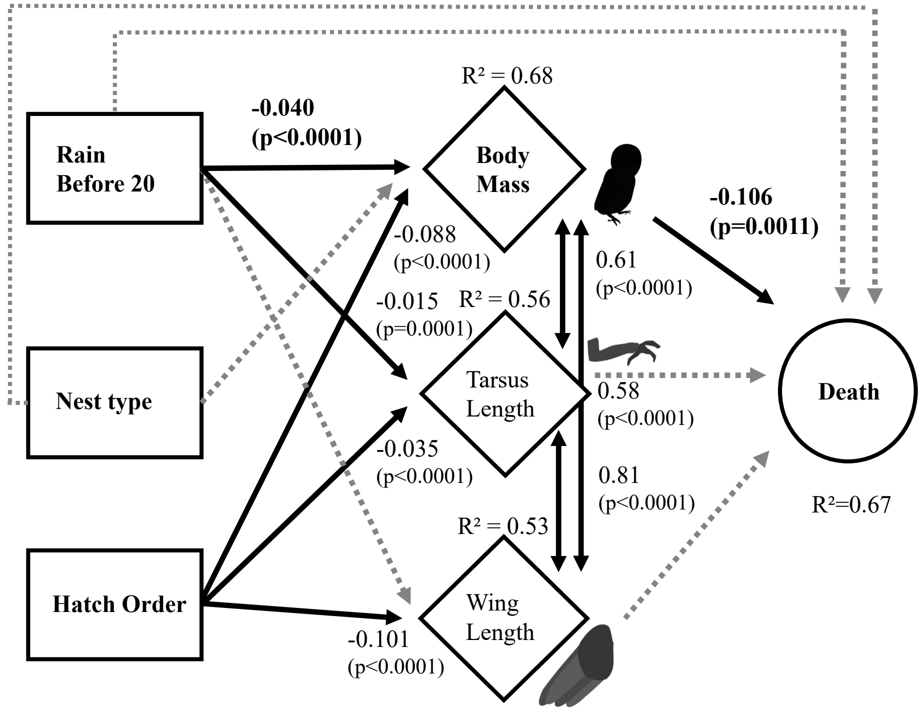

Fig. 3. Structural Equation modelling for analyzing the causes of chick mortality. Statistically significant paths are indicated by solid lines with their coefficients. Statistically non-significant paths are indicated by dotted lines. Estimated coefficients and p-values for significant paths and paths related to precipitation are indicated next to the arrows.

lower temperatures (Shiao et al. 2015). Regarding the effect of temperature, many studies have shown that higher temperatures have a positive effect on reproductive performance and growth rate in high latitude regions (Peery et al. 2012; Chausson et al. 2014; de Zwaan et al. 2019). Unlike in temperate zones, in the arid zone higher temperatures often reduce breeding success (Seamans et al. 2002; Peery et al. 2012; Comay et al. 2022). Even in tropical regions, high temperatures are known to have reduced bird survival (Woodworth et al. 2018). Chick mortality of Southern Pied Babbler *Turdoides bicolor*, a bird which inhabits the arid regions of Africa, increases dramatically when temperatures exceed 35.4°C (Bourne et al. 2020). These examples suggest that too high temperatures are detrimental to bird breeding. In the subtropics, it is possible that there is no clear linear relationship between temperature and mortality because of the negative effects of low temperatures as well as a few negative effects of high temperatures, as temperatures are higher than in temperate zones. In the future, as global warming progresses and temperatures rise, there is a risk that mortality rates will increase drastically.

In our study, analysis of chick survival showed that mortality was lower at lower wind speeds. However, the effect of wind speed could not be detected in the analysis of morphology. Many studies have focused on the effects of temperature and precipitation, and only a few papers have detected the effects of wind speed (Weimerskirch et al. 2012). In many cases, wind speed is known to have a negative effect on reproduction, with higher wind speeds reducing chick growth (McCarty & Winkler 1999; Mainwaring & Hartley 2016) and higher levels of stress hormones (Crino et al. 2020). These are related to the effects of windy conditions that reduce parental foraging ability or that increase noise stress. A rare example of a positive influence from wind speed is that of the Wandering Albatross *Diomedea exulans*, where strong wind speed in a particular direction increases feeding efficiency and improves breeding success (Weimerskirch et al. 2012). However, given the extremely different ecology of albatrosses foraging in the pelagic zone, it is unlikely that Ryukyu Scops Owls benefit from wind speeds through a similar mechanism because they live in forests and travel short distances. It is known that insects sometimes concentrate downwind of windbreaks when wind speeds are high (Verboom & Spoelstra 1999), and some wind speed may increase the foraging efficiency of owls. However, this trend should be considered with caution, as it was not consistent across all analyses. Future research should involve a detailed re-evaluation of these findings.

2) Differential effects of weather conditions on growth for different morphological traits

Precipitation affected chick weight, tarsus and wing growth. Higher precipitation commonly leads to smaller body sizes (Pérez et al. 2016), likely due to reduced feeding opportunities during bad weather, affecting food availability (Cox et al. 2019; Grzędzicka 2019). Given that the effect of precipitation on wing length was not significant in SEM analysis, wing length was less affected by precipitation than weight and tarsus length. Wing length grows slower than other parts of the body and was still growing at 20 days of age when measurements were taken (Sawada et al. 2021). If birds leave the nest with underdeveloped wings, their flight ability is low and the risk of death is increased (Jones & Ward 2020). Furthermore wing growth may be prioritized over weight if there is a risk of delayed fledging (Cheng & Martin 2012; Cunningham et al. 2013). In other words, they were growing their wings in spite of unfavourable weather conditions in order to avoid any delay in fledging.

3) How does precipitation impact chick survival

The structural equation model allows for the separation of direct and indirect effects of weather conditions (Bourne et al. 2020; van de Ven et al. 2020). Higher precipitation, before measurement, caused lighter weight, and indirectly affected mortality. Therefore, it was thought that the chicks were not dying from hypothermia (Anctil et al. 2014), but from starvation because of heavy rains that interfered with parental feeding (Pérez et al. 2016; Cox et al. 2019). Seabird chicks respond to temporary food shortages by lowering their body temperature and metabolism (Kuepper et al. 2018). However, in owl species, adult birds are only known to adapt to starvation by hypothermia in winter (Chaplin et al. 1984; Smit & McKechnie 2010). Under cooler conditions, the risk of hypothermia is known to increase and the effects of precipitation are more pronounced (Martin et al. 2017). The fact that nestlings were affected more indirectly rather than directly by precipitation can probably be related to the higher temperature of subtropical regions and a lower risk of hypothermia.

Not only precipitation but hatching order also influenced chick weight. Thus, chicks that hatched later were more likely to die after heavy rainfall. A reduction in brood size would increase the food available to the surviving chicks, thus decreasing the mortality of the remaining individuals. This suggests that the strategy of asynchronous hatching facilitates improved reproductive success even when weather conditions are unfavourable (Takagi 2001).

Research into the mechanisms by which weather conditions affect birds has been increasingly conducted in recent years on a variety of species, some using SEM analysis (Bourne et al. 2020; van de Ven et al. 2020) and others taking an experimental approach (Wada et al. 2015; Rodríguez & Barba 2016; Ospina et al. 2018). In a similar study of birds in arid regions, precipitation affected mortality directly (Bourne et al. 2020). This may reflect the fact that the mechanism by which mortality is affected by precipitation, differs between subtropical and arid regions. In American Kestrel *Falco sparverius* and Eurasian Hoopoe *Upupa epops*, it was found that parental feeding frequency or the amount of feeding was reduced and chick mortality increased when precipitation was higher (Dawson & Bortolotti 2000; Arlettaz et al. 2010), and our results may be due to this mechanism. Converseley, inclement weather is known to elevate corticosterone, a known stress hormone (Wingfield et al. 2017; Mikkelsen et al. 2022), and it is possible that weather conditions affect morphological traits through increased corticosterone. More research that considers not only climatic conditions but also morphology, feeding rates, and physiological conditions, would improve our understanding of the mechanism by which weather conditions affect birds from different regions and ecologies.

4) Conclusion

Based on analyses of the effects of weather conditions on the breeding success of Ryukyu Scops Owls on a subtropical island, it can be concluded that negative effects on breeding success of birds in the subtropics are similar to those in the temperate zone. However, the effects of low temperatures were unclear. And the mechanism by which high precipitation adversely affects mortality was considered to be indirect, via a reduction in body weight.

ACKNOWLEDGMENTS

We gratefully acknowledge the work of past and present members of our laboratory. We are grateful to Kiyoshi Asanuma, Mitsunori Okuyama, Tomiko Okuyama, Michiko Yamakawa, Kazuaki Higashi, Yui Henza, Shigeru Okiyama, Morio Kinjo, Jun-ichi Gima and Reiko Gima for kindly supporting our field research. This study was funded from the Seven-Eleven Midori no Kikin (Seven-Eleven Foundation), Tokyo Zoological Park Society Wildlife Conservation Fund (Tokyo Zoological Park Society), Pro-Nature Foundation (The Nature Conservation Society of Japan), Montbell Club Fund, Bird Research Support Project, Inui Memorial Trust for Research on Animal Science, The Zoshinkai Fund for Protection of Endangered Animals, and a Sasakawa Scientific Research Grant from the Japan Science Society and Grant-in-Aid for JSPS Research Fellow (Grant Number 16H04737 and 19J12833).

REFERENCES

Akatani K, Matsuo T & Takagi M (2011) Breeding ecology and habitat use of the daito scops owl (*Otus elegans interpositus*) on an oceanic Island. J Raptor Res 45: 315–323.

Akatani K & Takagi M (2020) Remigial and rectricial molt sequences in a captive Ryukyu Scops-Owl (*Otus elegans*). Wilson J Ornithol 131: 828–833.

Anctil A, Franke A & Bêty J (2014) Heavy rainfall increases nestling mortality of an arctic top predator: Experimental evidence and long-term trend in peregrine falcons. Oecologia 174: 1033–1043.

Anezak S (2012) Avifauna of Kita-daito Island and Minami-daito Island before World War II. J Yamashina Inst Ornithol 43: 105–151.

Arlettaz R, Schaad M, Reichlin TS & Schaub M (2010) Impact of weather and climate variation on Hoopoe reproductive ecology and population growth. J Ornithol 151: 889–899.

Bartoń K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. Available at https://CRAN.R-project.org/package=MuMIn (accessed on 6 December 2022).

Bates D, Mächler M, Bolker BM & Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67.

Bender IMA, Kissling WD, Böhning-Gaese K, Hensen I, Kühn I, Nowak L et al. (2019) Projected impacts of climate change on functional diversity of frugivorous birds along a tropical elevational gradient. Sci Rep 9: 1–12.

Bourne AR, Cunningham SJ, Spottiswoode CN & Ridley AR (2020) High temperatures drive offspring mortality in a cooperatively breeding bird: Temperature drives offspring mortality. Proc R Soc B Biol Sci 287: 20201140.

Brawn JD, Angehr G, Davros N, Robinson WD, Styrsky JN & Tarwater CE (2011) Sources of variation in the nesting success of understory tropical birds. J Avian Biol 42: 61–68.

Chaplin SB, Diesel DA & Kasparie JA (1984) Body temperature regulation in red-tailed hawks and great horned owls: responses to air temperature and food deprivation. Condor 86: 175–181.

Charmantier A & Gienapp P (2014) Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. Evol Appl 7: 15–28.

Chausson A, Henry I, Almasi B & Roulin A (2014) Barn Owl (*Tyto alba*) breeding biology in relation to breeding season climate. J Ornithol 155: 273–281.

Cheng YR & Martin TE (2012) Nest predation risk and growth strategies of passerine species: Grow fast or develop traits to escape risk? Am Nat 180: 285–295.

Comay O, Ezov E, Yom-Tov Y & Dayan T (2022) In Its Southern Edge of Distribution, the Tawny Owl (*Strix aluco*) Is More Sensitive to Extreme Temperatures Than to Rural Development. Animals 12: 641.

Cox AR, Robertson RJ, Lendvai AZ, Everitt K & Bonier F (2019) Rainy springs linked to poor nestling growth in a declining avian aerial insectivore (*Tachycineta bicolor*). Proc R Soc B Biol Sci 286: 20190018.

Crino OL, Driscoll SC, Brandl HB, Buchanan KL & Griffith SC (2020) Under the weather: Corticosterone levels in wild nestlings are associated with ambient temperature and wind. Gen Comp Endocrinol 285: 113247.

Cunningham SJ, Martin RO, Hojem CL & Hockey PAR (2013) Temperatures in Excess of Critical Thresholds Threaten Nestling Growth and Survival in A Rapidly-Warming Arid Savanna: A Study of Common Fiscals. PLoS One 8(9): e74613.

Dawson RD & Bortolotti GR (2000) Reproductive success of American Kestrels: The role of prey abundance and weather. Condor 102: 814–822.

de Zwaan DR, Camfield AF, MacDonald EC & Martin K (2019) Variation in offspring development is driven more by weather and maternal condition than predation risk. Funct Ecol 33: 447–456.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC et al. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci USA 105: 6668–6672.

Feeley KJ, Stroud JT & Perez TM (2017) Most 'global' reviews of species' responses to climate change are not truly global. Divers Distrib 23: 231–234.

Fisher RJ, Wellicome TI, Bayne EM, Poulin RG, Todd LD & Ford AT (2015) Extreme precipitation reduces reproductive output of an endangered raptor. J Appl Ecol 52: 1500–1508.

Fox J & Weisberg S (2019) An {R} Companion to Applied Regression, Third Edition. Sage, Thousand Oaks CA.

Freeman BG & Class Freeman AM (2014) Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. Proc Natl Acad Sci USA 111: 4490–4494.

Freeman BG, Scholer MN, Ruiz-Gutierrez V & Fitzpatrick JW (2018) Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. Proc Natl Acad Sci USA 115: 11982–11987.

Gill F, Donsker D & Rasmussen P (2023) IOC World Bird List (v13.2). Available at https://www.worldbirdnames.org/new/ (accessed on 7 December 2023).

Gordo O & Doi H (2012) Spring phenology delays in an insular subtropical songbird: is response to climate change constrained by population size? J Ornithol 153: 355–366.

Grzędzicka E (2019) Impact of rainfall on the offspring PHA-response and body mass in the Eurasian blue tit. Ecol Res 34: 85–93.

Hidalgo Aranzamendi N, Hall ML, Kingma SA, van de Pol M & Peters A (2019) Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. J Anim Ecol 88: 1799–1811.

Japan Meteorological Agency (2022) Historical weather data retrieval. Available at https://www.data.jma.go.jp/obd/stats/etrn/index.php (accessed on 6 August 2021).

Jones TM & Ward MP (2020) Pre- to post-fledging carryover effects and the adaptive significance of variation in wing development for juvenile songbirds. J Anim Ecol 89: 2235–2245.

Kenny DA, Kaniskan B & McCoach DB (2015) The Performance of RMSEA in Models With Small Degrees of Freedom. Sociol Methods Res 44: 486–507.

Kuepper ND, Marek C, Coria N, Libertelli MM & Quillfeldt P (2018) Facultative hypothermia as a survival strategy during snowstorm induced food shortages in Antarctic storm-petrel chicks. Comp Biochem Physiol -Part A Mol Integr Physiol 224: 76–83.

Lefcheck JS (2016) piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol Evol 7: 573–579.

Lima M, Stenseth NC & Jaksic FM (2002) Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecol Lett 5: 273–284.

Liu CY, Gélin U, He RC, Li H & Quan RC (2021) Flexible breeding performance under unstable climatic conditions in a tropical passerine in Southwest China. Zool Res 42: 221–226.

Mainwaring MC & Hartley IR (2016) Local weather conditions have complex effects on the growth of blue tit nestlings. J Therm Biol 60: 12–19.

Martin K, Wilson S, Macdonald EC, Camfield AF, Martin M & Trefry SA (2017) Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: Interactions of climate extremes influence nesting success. Auk 134: 696–709.

McCarty JP & Winkler DW (1999) Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. Ibis (Lond 1859) 141: 286–296.

Mikkelsen AJ, Lesmeister DB, O'Reilly KM & Dugger KM (2022) Feather corticosterone reveals developmental challenges in a long-term study of juvenile northern spotted owls. Funct Ecol 36: 51–63.

Ministry of the Environment (2020) Ministry of the Environment Red List 2020. Available at https://www.env.go.jp/press/107905.html (accessed on 6 August 2021).

Neate-Clegg MHC, Jones SEI, Tobias JA, Newmark WD & Şekercioğlu ÇH (2021) Ecological Correlates of Elevational Range Shifts in Tropical Birds. Front Ecol Evol 9: 1–16.

Oppel S, Hilton GM, Allcorn R, Fenton C, Matthews AJ & Gibbons DW (2013) The effects of rainfall on different components of seasonal fecundity in a tropical forest passerine. Ibis (Lond 1859) 155: 464–475.

Ospina EA, Merrill L & Benson TJ (2018) Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. Ecol Evol 8: 3270–3279.

Peery MZ, Gutiérrez RJ, Kirby R, Ledee OE & Lahaye W (2012) Climate change and spotted owls: Potentially contrasting responses in the Southwestern United States. Glob Chang Biol 18: 865–880.

Pérez JH, Krause JS, Chmura HE, Bowman S, McGuigan M, Asmus AL et al. (2016) Nestling growth rates in relation to food abundance and weather in the Arctic. Auk 133: 261–272.

Rodríguez S & Barba E (2016) Nestling growth is impaired by heat stress: An experimental study in a mediterranean great tit population. Zool Stud 55: 40.

Salaberria C, Celis P, López-Rull I & Gil D (2014) Effects of temperature and nest heat exposure on nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. Ibis (Lond 1859) 156: 265–275.

Sawada A, Akatani K & Takagi M (2021) Growth Curves of Ryukyu Scops Owl Nestlings, an Owl Species with Asynchronous Hatching and Reversed Sexual Dimorphism. Ardea 109: 1–13.

Scheffers BR, De Meester L, Bridge TCL, Hoffmann AA, Pandolfi JM, Corlett RT et al. (2016) The broad footprint of climate change from genes to biomes to people. Science 354(6313): aaf7671.

Seamans ME, Gutiérrez RJ & May CA (2002) Mexican Spotted Owl (*Strix occidentalis*) population dynamics: Influence of climatic variation on survival and reproduction. Auk 119: 321–334.

Senapathi D, Nicoll MAC, Teplitsky C, Jones CG & Norris K (2011) Climate change and the risks associated with delayed breeding in a tropical wild bird population. Proc R Soc B Biol Sci 278: 3184–3190.

Sheldon KS, Huey RB, Kaspari M & Sanders NJ (2018) Fifty years of mountain passes: A perspective on Dan Janzen's classic article. Am Nat 191: 553–565.

Shiao MT, Chuang MC, Yuan HW & Wang Y (2015) Effects of weather variation on the timing and success of breeding in two cavity-nesting species in a subtropical montane forest in Taiwan. Auk 132: 671–684.

Shiao MT, Chuang MC, Yuan HW & Wang Y (2020) Seasonal rainfall in subtropical montane cloud forests drives demographic fluctuations in a Green-backed Tit population. Condor 122: 1–15.

Smit B & McKechnie AE (2010) Do owls use torpor? Winter thermoregulation in free-ranging pearl-spotted owlets and african scops-owls. Physiol Biochem Zool 83: 149–156.

Styrsky JN & Brawn JD (2011) Annual fecundity of a neotropical bird during years of high and low rainfall. Condor 113: 194–199.

Takagi M (2001) Some effects of inclement weather conditions on the survival and condition of bull-headed shrike nestlings. Ecol Res 16: 55–63.

Takagi M, Akatani K, Matsui S & Saito A (2007) Status of the Daito Scops Owl on Minami-Daito Island, Japan. J Raptor Res 41: 52–56.

Takagi M, Saitoh T, Yamaguchi N, Okabe H, Nishiumi I & Takeishi M (2015) A breeding record of the Ryukyu Scops Owl on Okinoshima, in northernmost Fukuoka, Japan. Ornithol Sci 14: 53–59.

Tarwater CE & Beissinger SR (2013) Opposing selection and environmental variation modify optimal timing of breeding. Proc Natl Acad Sci USA 110: 15365–15370.

Taylor J, Nicoll MAC, Black E, Wainwright CM, Jones CG, Tatayah V et al. (2021) Phenological tracking of a seasonal climate window in a recovering tropical island bird species. Clim Change 164: 1–19.

van de Ven TMFN, McKechnie AE, Er S & Cunningham SJ (2020) High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird. Oecologia 193: 225–235.

Verboom B & Spoelstra K (1999) Effects of food abundance and wind on the use of tree lines by an insectivorous bat, Pipistrellus pipistrellus. Can J Zool 77: 1393–1401.

Wada H, Kriengwatana B, Allen N, Schmidt KL, Soma KK & MacDougall-Shackleton SA (2015) Transient and permanent effects of suboptimal incubation temperatures on growth, metabolic rate, immune function and adrenocortical responses in zebra finches. J Exp Biol 218: 2847–2855.

Weimerskirch H, Louzao M, De Grissac S & Delord K (2012) Changes in wind pattern alter albatross distribution and life-history traits. Science (80-) 335: 211–214.

Wingfield JC, Pérez JH, Krause JS, Word KR, González-Gómez PL, Lisovski S et al. (2017) How birds cope physiologically and behaviourally with extreme climatic events. Philos Trans R Soc B Biol Sci 372: 20160140.

Winkler DW, Luo MK & Rakhimberdiev E (2013) Temperature effects on food supply and chick mortality in tree swallows (Tachycineta bicolor). Oecologia 173: 129–138.

Woodworth BK, Norris DR, Graham BA, Kahn ZA & Mennill DJ (2018) Hot temperatures during the dry season reduce survival of a resident tropical bird. Proc R Soc B Biol Sci 285: 2018176.

SUPPORTING INFORMATION

Supporting information is available with the online version of this article.