



Synchronizing biological cycles as key to survival under a scenario of global change: The Common quail (*Coturnix coturnix*) strategy



Jesús Nadal^{a,*}, Carolina Ponz^a, Antoni Margalida^{a,b}

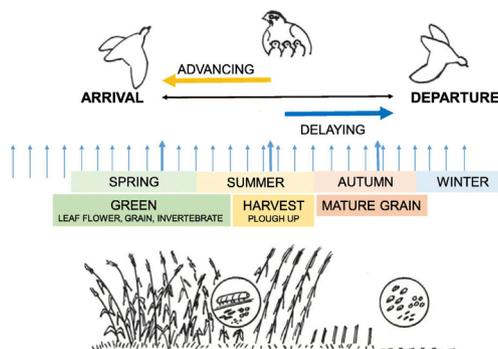
^a Department of Animal Science, Division of Wildlife, Faculty of Life Sciences and Engineering, University of Lleida, 25198 Lleida, Spain

^b Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, 3012 Bern, Switzerland

HIGHLIGHTS

- The impact of climate warming and farming practices on quail phenology is unknown.
- We use a long-term study (1961–2014) of quail-ringing in Spain and data on variation in rainfall and temperature.
- Our results suggest that increases in temperature and decreases in precipitation modify quail phenology.
- Quail movements and breeding attempts are eco-synchronized sequentially in cloudy regions.
- Quails attempt to overcome the negative impacts by searching for alternative high-quality habitats.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 18 August 2017

Received in revised form 16 September 2017

Accepted 16 September 2017

Available online xxxx

Editor: D. Barceló

Keywords:

Agricultural intensification
Habitat quality
Phenological changes
Sustainability
Synchronizing strategy
Weather effects

ABSTRACT

Breeding grounds are key areas for sustaining Common quail (*Coturnix coturnix*) populations as this species is characterised by short life expectancy that requires high offspring production. Annually, breeding quails make up to three breeding attempts in different places. However, the impact of climate warming on quail phenology is unknown. Here, we use a long-term study (1961–2014) of quail-ringing in Spain and data on variation in rainfall and temperature over the past 86 years to evaluate how quails have responded to climate change in recent years. Our aim was to understand how this species is adapting to new farming practices and climate change. Our results suggest that increases in temperature and decreases in precipitation modify quail phenology. In hot years, an advance in mean arrival dates and stay stages but a delay in departure dates was found. However, in rainy years a delay in the mean start of the stay stage occurred. In cloudy areas, our findings show that quails advance their stay periods in hot and dry years and delay them in cold and rainy years. Accordingly, quail movements and breeding attempts are eco-synchronized sequentially in cloudy regions. Our results suggest that quails attempt to overcome the negative impacts of climate change and agricultural intensification by searching for alternative high-quality habitats. This strategy could explain how quail populations maintain viable and sustainable populations despite being legally harvested with regulated hunting.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Climate change is a major threat to biodiversity and is provoking greater and accelerating extinction risks (Cahill et al., 2012; Pacifici et al., 2015; Urban, 2015). Species vulnerability is greatly affected by global

* Corresponding author.
E-mail address: jnadal@ca.udl.cat (J. Nadal).

change and in most cases conservation statuses will depend on an organism's adaptive capacity (Langham et al., 2015; Wade et al., 2017). However, the speed of change places a limit on adaptive capacity and biodiversity (Bateman et al., 2016; Boucher-Lalonde et al., 2014; Chen et al., 2011). Breeding and wintering areas are closely linked to the life history of migratory species. Warming favours some populations and species but is handicap for others – depending on their behaviour, physiology, habitats and, in particular, geographical distribution (Hughes, 2000; Marra et al., 2015). Farmland birds and cold habitats are most negatively affected by global change due to the shift to poorer habitat quality (Jørgensen et al., 2016; Rushing et al., 2016). As a result, altered habitats are having a serious impact on species interactions and the structure and function of ecological communities (Blois et al., 2013; Isbell et al., 2015; Savo et al., 2016).

Previous research into the effects of global change on migratory birds have documented, among other factors, how phenology mismatches lead to a desynchronization within biological cycles due to changes in arrival and departure dates (Ge et al., 2015; McDermott and DeGroote, 2016); this will have implications for niches and food availability (Jezkova and Wiens, 2016; Thorup et al., 2017) in both breeding and wintering areas and provoke changes in habitat quality (Ahola et al., 2004; Sanz et al., 2003). Warming affects birds in many ways such as how the photoperiod triggers migration and reproduction since temperature has regulatory effects on both these factors (Jenouvrier, 2013; Singh et al., 2012). Food mismatch is an important ecological problem for bird reproduction as species eco-synchronize the hatching and growth of chicks with abundance peaks in optimal food sources such as plant products, caterpillars, grasshoppers, flies and other invertebrates (Studds and Marra, 2011; Visser and Both, 2005). Arriving earlier and departing later is the most likely adaption to warming employed by summer migrant birds (Jonzén et al., 2007).

The Common quail (*Coturnix coturnix*) is an Afro-Palearctic migratory bird with a broad continental distribution. Certain individuals exhibit sedentary lifestyles, while others are short- or long-distance migrants. Quails inhabit pastures and farmland, and have an intricate life strategy: winter nomadism, spring migration, sequential breeding and autumn migration (Rodríguez et al., 2009). The Western Palearctic population begins breeding (first attempts) in North Africa and southern Spain; second attempts take place mainly in Spain, while third attempts are generally in Spain and Central Europe. As a result, Spain is a key area in the breeding strategy of this quail population and so knowledge of the effects of warming and intensive farming are essential if we are to understand changes occurring in the biology of this and other migratory birds.

Here, we use data from a long-term study (1961–2014) of quail-ringing in Spain and a vast meteorological data set (1930–2015) of

variation in rainfall and temperature in Spain over the past 86 years to evaluate how quails are responding to climate change. Our overall aim was to understand how this species is adapting to alterations in farming practices and climate change.

2. Methods

2.1. Ecology of the species

As shown in Fig. 1, climate has the effect of advancing or delaying biological cycles (Gordo et al., 2005; Knudsen et al., 2007; Peñuelas et al., 2002) and so climate change may modify the arrival and departure dates of migratory birds. In some species warming leads to the advancing of the date of arrival and a delay in the date of departure (Cruz-McDonnell and Wolf, 2016; Macmynowski et al., 2007). Climate has a direct influence on the ability of quails to find food (abundance of grain and invertebrates) and on the likelihood of predation (cover density), and also affects physiology and behaviour (Gillson et al., 2013; Madliger and Love, 2016). Starvation and predation risk are mutually dependent (Ockendon et al., 2014; Scheffers et al., 2016) and both have an impact on physiology and behaviour (Bulla et al., 2016; Mariette et al., 2015). Survival depends on a balance between starvation and the predation risk, as well as on physiological condition (health) and behavioural responses (experience) to daily challenges (Bonter et al., 2013; Hethcoat and Chalfoun, 2015).

Migratory quail move through different landscapes seasonally, exploiting shifting environmental resources and taking advantage of patches with abundant food (Somveille et al., 2015; Zuckerberg et al., 2016). Quails' annual cycle can be divided into four biological stages: winter, pre-nuptial migration (arrival), breeding stays, and post-nuptial migration (departure); in Spain, arrivals take place in February–April, breeding stays last through May–July and departures occur in August–October. Quails link habitat quality to population demography via movement patterns (Taylor et al., 2016), and initially follow agricultural greenup for breeding but then abandon reproduction sites when cereals are harvested (Fig. 2). Mismatches can occur when components of the biological cycle such as hatching dates and food supply for chicks become desynchronized (Saino et al., 2011).

In earlier research designed to select the variables that most influence and explain the data in the quail-ringing database, agriculture-related variables (dry or irrigated land) were discarded due to their small (non-significant) contribution to the model (logistic regression). However, agrosystems are associated and affected by cloudy areas, defined as geographic areas with similar level of cloud coverage (Appendix Fig. 7).

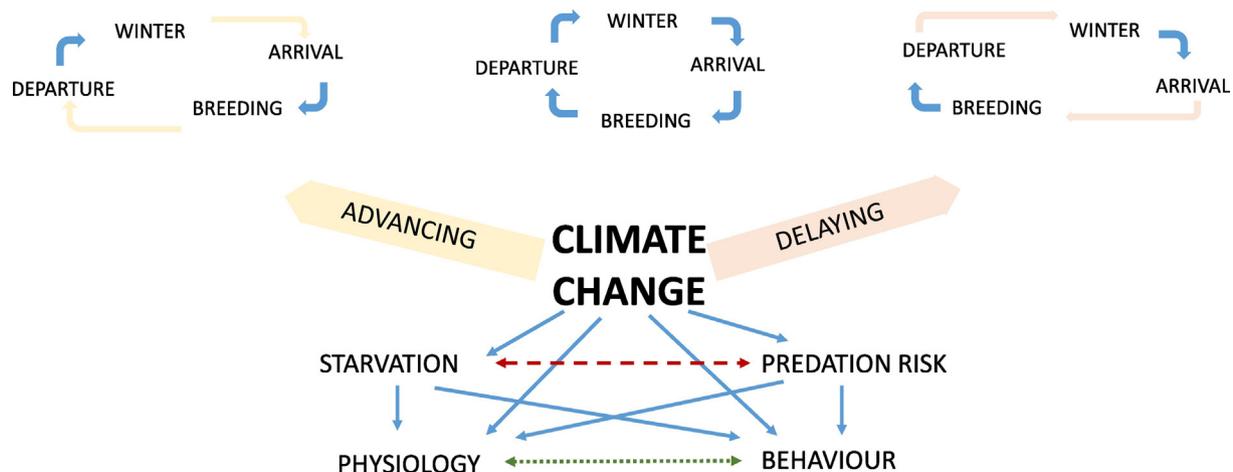


Fig. 1. Hypothetical quail biological cycle framework related to climate effects. Warming causes the advance of dates of spring migration and a delay in autumn return, which in turn modify ecological balances.

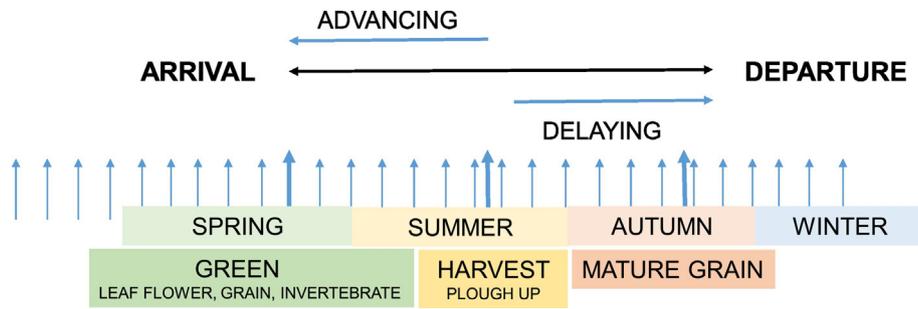


Fig. 2. Synchronization of the biological cycle of quail with plant growth. Advances and delays in quail migration and possible effects on breeding. Vertical arrows are time units (15 days), thick arrows indicate arrival (February–April), stay (May–July) and departure (August–October) quail stages in Spain.

2.2. Data collection

We used quail ringing data consisting of 43,194 records (Table 1) from a number of ringing schemes: 37,706 records from SEO/BirdLife (ICONA rings), 4209 records from hunting associations (FEDENCA rings) and two autonomous communities (Junta de Castilla y León and Cabildo de Tenerife rings), and 1279 records from the Sociedad de Ciencias Aranzadi (ARANZADI rings) covering the period 1961–2014. We filtered and homogenized these datasets to generate standardized information that included Julian date, longitude, latitude and altitude according to Nomenclator (IGN, 2015) of the ringing locality, and habitat (dry land or irrigated land). The temporal and spatial distribution of ringing teams were associated with the presence and abundance of quail in the territory. Given that this study does not attempt to evaluate quail abundance using ringing data and the fact that sample sizes at each stage are important, the differences in ringing effort should not affect our results.

We obtained rainfall and temperature data from AEMET (the Spanish Meteorological Office) consisting of 2,724,261 monthly rainfall records from 10,834 stations, and 1,045,137 average monthly temperature records from 5332 stations. We then built a meteorological database for the eight cloudiest Spanish regions according to the maps in Wilson and Jetz (2016). In each geographic area (cloudy region) and year, we used all the assigned stations to obtain monthly averages for temperature and rainfall, and then calculated the average temperature and rainfall for the three biological stages (arrival: February–April, stay: May–July; departure: August–October; Fig. 2). Finally, we matched the ringing database with the meteorological database and each quail record (i.e. location and date of capture) was assigned the climate data corresponding to the average for the geographic region in that month, stage and year.

2.3. Statistical analyses

We calculated the mean Julian date for each stage (arrival, breeding stay and departure) for Spain and for cloudy areas, as well as monthly and annual mean precipitation, and temperature for each stage in Spain and in geographic areas. Then, for each cloudy area we obtained mean precipitation and temperature figures for each period (arrival: February–April, stay: May–July; departure: August–October). Following the same process, we also calculated the mean Julian ringing date for

each geographic area (Canary Islands, Ceuta–Melilla, Centro-Sur, Balearic Islands, North Plateau, North, Duero Valley, Ebro Valley). We built simple regression models with meteorological variables (year and mean) and the Julian date of ringing. We used JMP11 (SAS, 2015) to statistically analyse the studied variables.

3. Results

Over the past 86 years, precipitation in Spain has decreased significantly during the stay stage (May–July) ($R^2 = 0.12$, $F = 11.48$, $P < 0.001$, $n = 86$) but not for arrival (February–April) ($R^2 = 0.01$, $F = 0.9$, $P > 0.35$, $n = 86$) or departure (August–October) periods ($R^2 = 0.002$, $F = 0.14$, $P > 0.75$, $n = 86$ Fig. 3). In the stay stage, with increased precipitation, the mean date of quail ringing was delayed significantly ($R^2 = 0.24$, $F = 50.72$, $P < 0.001$, $n = 164$); however, no relationship was found between increased precipitation and either arrival ($R^2 = 0.002$, $F = 0.25$, $P > 0.62$, $n = 143$) or departure ($R^2 = 0.001$, $F = 0.13$, $P > 0.72$, $n = 108$ Fig. 4).

In the last 86 years, temperatures have increased significantly for arrival ($R^2 = 0.12$, $F = 11.25$, $P < 0.001$, $n = 86$), stay ($R^2 = 0.15$, $F = 15.34$, $P < 0.0002$, $n = 86$) and departure ($R^2 = 0.16$, $F = 16.18$, $P < 0.0001$, $n = 86$) stages. The arrival stage – that is, the mean Julian date of ringing – advanced significantly with increased temperature ($R^2 = 0.25$, $F = 45.69$, $P < 0.001$, $n = 143$); the stay stage – mean Julian date of ringing – advanced in accordance with increases in temperature ($R^2 = 0.35$, $F = 86.58$, $P < 0.0001$, $n = 164$); and the mean Julian date of ringing for the departure stage was delayed significantly with increases in temperature ($R^2 = 0.23$, $F = 30.69$, $P < 0.0001$, $n = 108$ Figs. 5 and 6, Table 2).

4. Discussion

Our results confirm an increase in temperatures in Spain in three stages of quail life histories: arrival (February–April), stay (May–July) and departure (August–October), as well as a decrease in precipitation during the stay stage. By contrast, no significant differences were found in precipitation trends in relation to arrival and departure stages (Gordo and Sanz, 2010; Saino and Ambrosini, 2008). These findings are consistent with other warming indicators such as those of the climatic panel (IPCC, 2014), Northern Hemisphere ice sheets (Zhang et al., 2014), faster warming rates in recent years (Hausfather et al., 2017), the Agulhas current (Beal and Elipot, 2016), greenhouse gases (Snyder, 2016) and rainfall regimes in the Sahara (Tierney et al., 2017).

Our findings also agree with previous studies that indicate the earlier arrival of migratory birds on breeding grounds (Kullberg et al., 2015) and later departure dates (Rivalan et al., 2007). In warm years, quails advanced their mean arrival and stay dates, and delayed their departures. This is consistent with the findings of delays in mean dates of stay during rainy years. Advances and delays of dates in stages of biological cycle can be interpreted as quails' responses to thermal cues that enable them to adapt their biological cycle to habitat phenology (Both and

Table 1
Quail banded in Spain according to ringing organization and ring type.

Ring type	Period	N years	N quail banded	Rings/years
SEO-ICONA	1961–2014	39	37,706	967
ARANZADI	2000–2014	15	1279	85
FEDENCA-CA	2002–2014	13	4209	324
Total	1961–2014	39	43,194	1108

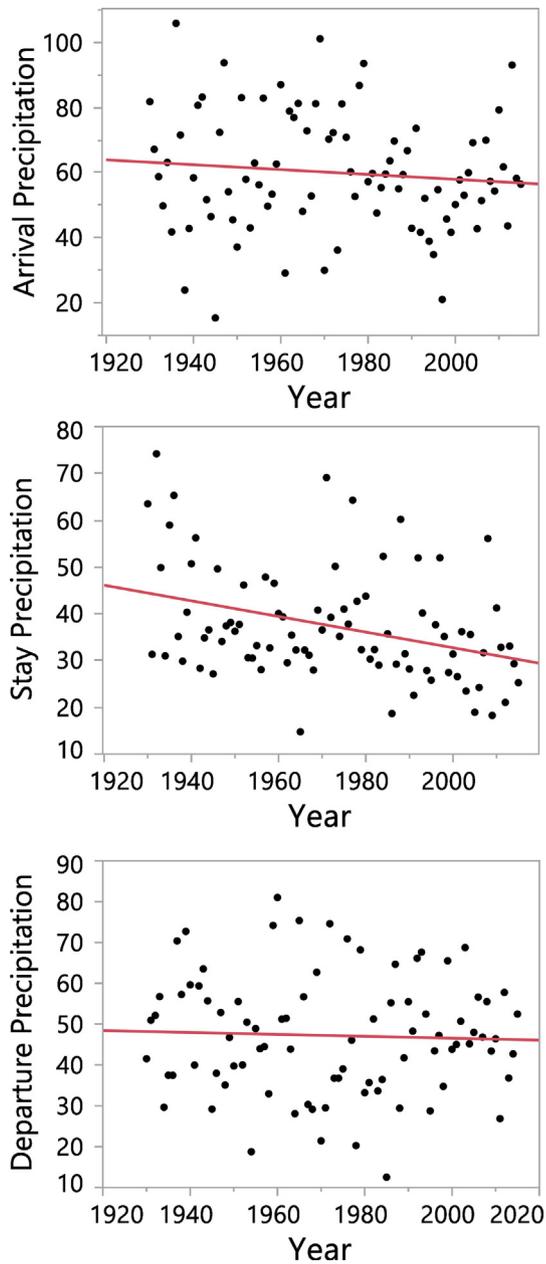


Fig. 3. Variation in mean monthly precipitation (mm) for arrival (February–April), stay (May–July) and departure (August–October) dates in Spain during the period 1930–2015.

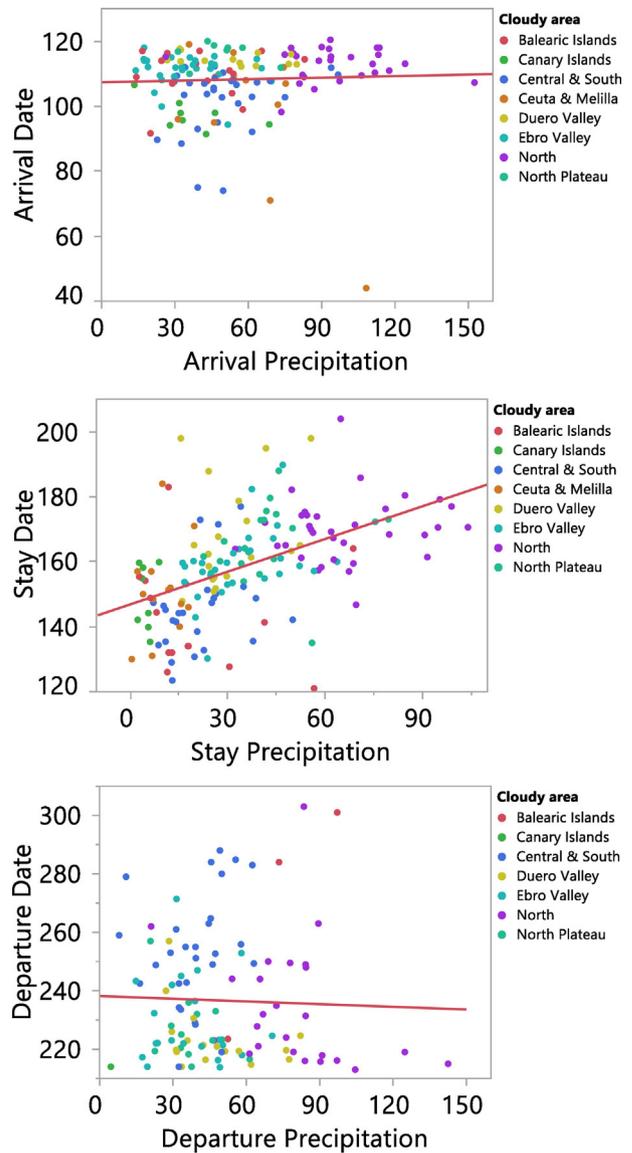


Fig. 4. Variation in mean the Julian date of quail ringing for arrival (February–April), stay (May–July) and departure (August–October) in Spain in relation to mean stage precipitation (mm). Colours show the different populations studied. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Visser, 2005). In this sense, many species of migratory birds face the problem of how to disengage their annual cycles from habitat cycles. Mismatches with habitat can lead to trophic-, cover-, mimetic- and eco-synchrony-related problems (Wiens et al., 2009; Ockendon et al., 2013). Accordingly, thermal delay has been suggested as one of the main drivers of population decline (Saino et al., 2011). On the other hand, thermal stress has been proposed as an important constraint on the use of space and survival rates (Tanner et al., 2017).

Thus, the study of long-term data series is key in understanding trends in global changes in biology (Conklin et al., 2010; Stephens et al., 2016). Long-term data series can also help understand stages of biological cycles. The ability of species to respond to new habitat conditions and their capacity to adjust will determine their vulnerability and their distribution limits (Goodenough and Hart, 2013; Moss et al., 2010). In particular, migration is an adaptive response to geographical and seasonal variation in resources (Small-Lorenz et al., 2013). Quail life strategies are characterised by sequential breeding and nomadic movements,

with females requiring 50 days for each breeding attempt; afterwards, they disperse in search of similar quality breeding habitat. We found that breeding stays and subsequent movements vary with precipitation and temperature in different geographic areas.

The data gathered for arrival, stay and departure stages suggest that precipitation and temperature have different impacts, although we found a negative relationship between precipitation and temperature that seems to vary with stages (Clement et al., 2016). During the stay stage (May–July), we found contrasting trends in precipitation and temperature (Miller-Rushing et al., 2008). For example, in warm and dry years, quails seem to advance stage dates to coincide with greenup and cereal maturation, while in cold and rainy years quails delay stage dates to eco-synchronize their breeding cycle with the ripening of herbaceous plants (Alexander et al., 2016). Habitat suitability changes with plant cycles and so quails occupy cloudy areas in sequential order in accordance with plant maturation over space and time. Quail follow a green wave of herbaceous plants (Sardà-Palomeya et al., 2012), although irrigated land with alfalfa, fodder and maize can also provide continuously green habitat for quails, albeit with limitations imposed

Table 2

Slopes from regression of rain and temperature with year, and with quail average dates \pm SD. Significant values in bold. Arrival: February–April; stay: May–July; departure: August–October.

Regression with year	b \pm SD	Regression with quail date	b \pm SD
Arrival precipitation and years	-0.07 \pm 0.08	Arrival precipitation and quail arrival date	0.02 \pm 0.03
Stay precipitation and years	-0.17 \pm 0.05	Stay precipitation and quail stay date	0.34 \pm 0.05
Departure precipitation and years	-0.02 \pm 0.06	Departure precipitation and quail departure date	-0.03 \pm 0.09
Arrival temperature and years	0.01 \pm 0.004	Arrival temperature and quail arrival date	-2.02 \pm 0.30
Stay temperature and years	0.02 \pm 0.004	Stay temperature and quail stay date	-4.29 \pm 0.46
Departure temperature and years	0.01 \pm 0.003	Departure temperature and quail departure date	4.66 \pm 0.84

by short cut cycles and the use of pesticides (Sax et al., 2013). Quails adapt to warm and cold years by modifying their sequential breeding patterns. Nevertheless, further research is still needed to better understand their capacity to adjust to major changes (Schaefer et al., 2008).

Land use limits the availability of suitable habitat for quails, while the likelihood of successful breeding is associated with cloudy areas and plant ripening. Quails have to synchronize their breeding attempts with plant cycles but also have to find a balance between starvation and predation risks, as well as their migration routes with resources and suitable climate. Temperature and greenness seem to be the most likely cues that indicate the suitability of a place and time for breeding (La Sorte and Fink, 2017). Conspecific and heterospecific interactions regulate reproduction opportunities, and there is evidence that migration

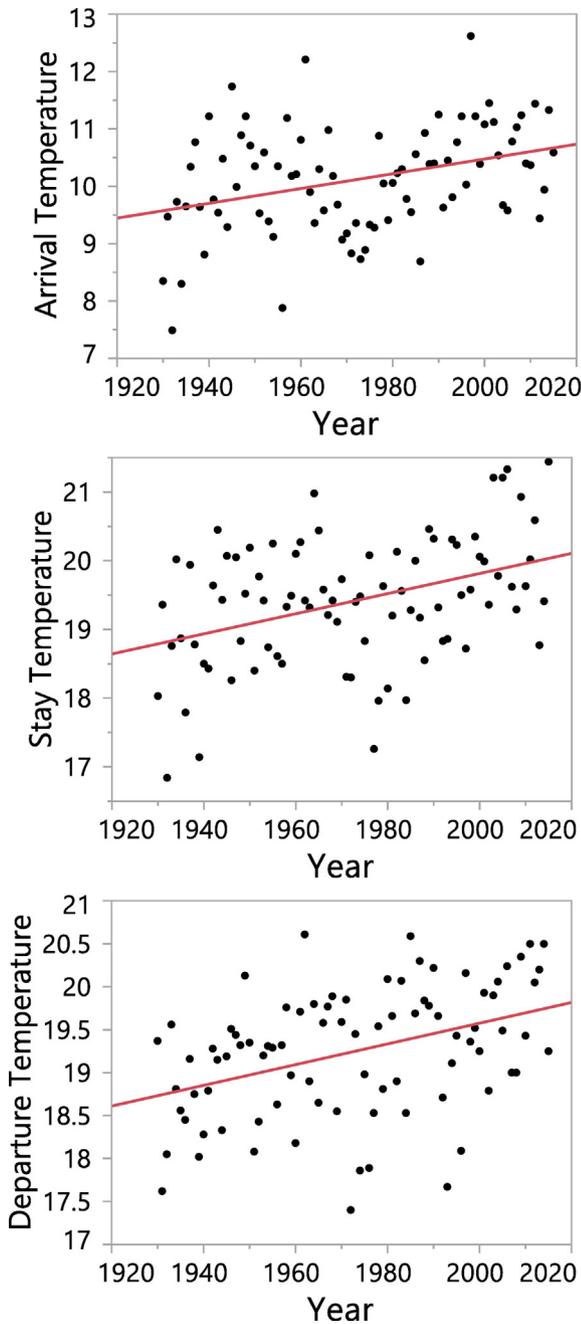


Fig. 5. Variation in mean monthly temperature (°C) for arrival (February–April), stay (May–July) and departure (August–October) dates in Spain in relation to years during the period 1930–2015.

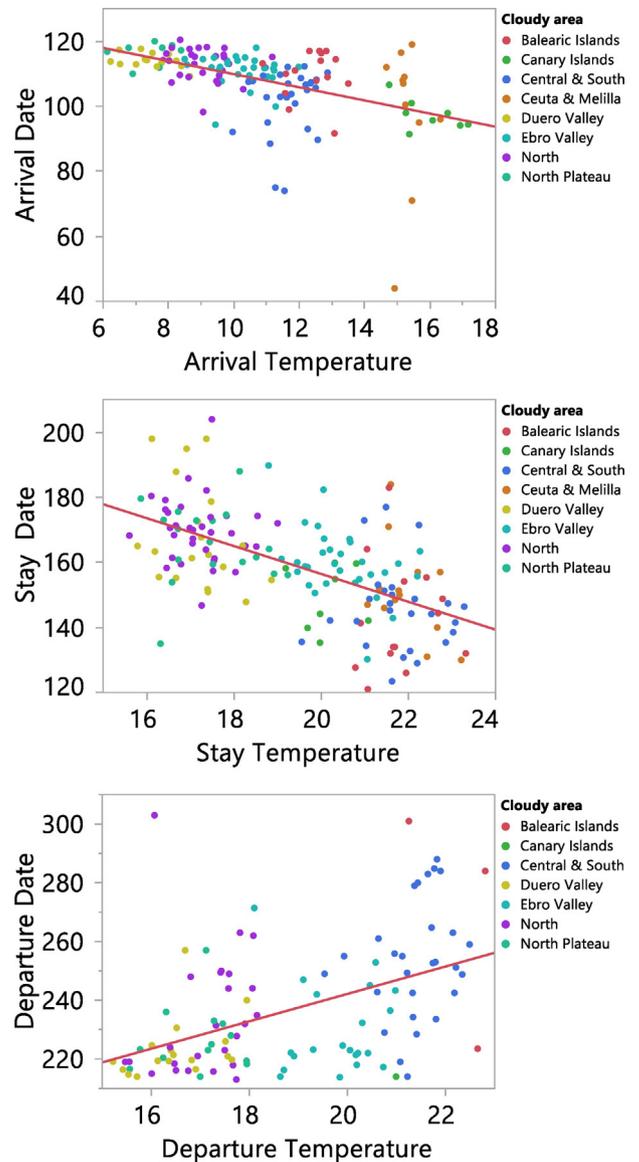


Fig. 6. Variation in the mean Julian date of quail ringing for arrival (February–April), stay (May–July) and departure (August–October) dates in Spain in relation to mean stage temperatures (°C).

and nomadism are strategies that maximize the probability of finding a mate and avoiding being misled (Martin and Maron, 2012). Warming and intensive farming reduce the chance of survival and successful breeding. Migratory species with more northerly ranges (polar or near the poles) do not have alternatives to their micro-refuges in the same range, and thus their populations are in decline (Lehikoinen and Virkkala, 2016). Physiological adaptation processes in the past took place over thousands of years, as did changes in geographical habitat. Thus, from a management and conservation perspective, we must mitigate warming and protect micro-refuges. Conserving, recovering and building quality habitats should be a top priority in tasks aimed at protecting migratory bird species.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2017.09.168>.

Acknowledgements

We are grateful to the SEO, ICO, ARANZADI, FEDENCA, FCCL, and AEMET for allowing the use of their banding and meteorological databases and contributions made by the hunters and their families, especially the Iturmendi family. The comments of two reviewers improved a previous version of this manuscript. A.M. was supported by a Ramón y Cajal research contract by the Ministry of Economy and Competitiveness (RYC-2012-11867).

References

- Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K., Lehikoinen, E., 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob. Chang. Biol.* 10: 1610–1617. <https://doi.org/10.1111/j.1365-2486.2004.00823.x>.
- Alexander, J.M., Diez, J.M., Hart, S.P., Levine, J.M., 2016. When climate reshuffles competitors: a call for experimental macroecology. *Trends Ecol. Evol.* 31:831–841. <https://doi.org/10.1016/j.tree.2016.08.003>.
- Bateman, B.L., Pidgeon, A.M., Radeloff, V.C., Vanderwal, J., Thogmartin, W.E., Vavrus, S.J., et al., 2016. The pace of past climate change vs. potential bird distributions and land use in the United States. *Glob. Chang. Biol.* 22:1130–1144. <https://doi.org/10.1111/gcb.13154>.
- Beal, L.M., Elipot, S., 2016. Broadening not strengthening of the Agulhas Current since the early 1990s. *Nature* 540:570–573. <https://doi.org/10.1038/nature19853>.
- Blois, J.L., Zametske, P.L., Fitzpatrick, M.C., Finnegan, S., 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341:499–504. <https://doi.org/10.1126/science.1237184>.
- Bonter, D.N., Zuckerman, B., Sedgwick, C.W., Hochachka, W.M., 2013. Daily foraging patterns in free-living birds: exploring the predation – starvation trade-off. *Proc. R. Soc. B* 280 (20123087). <https://doi.org/10.1098/rspb.2012.3087>.
- Both, C., Visser, M.E., 2005. The effect of climate change on the correlation between avian life-history traits. *Glob. Chang. Biol.* 11:1606–1613. <https://doi.org/10.1111/j.1365-2486.2005.01038.x>.
- Boucher-Lalonde, V., Kerr, J.T.J., Currie, D.J., 2014. Does climate limit species richness by limiting individual species' ranges? *Proc. R. Soc. B* 281:20132695. <https://doi.org/10.1098/rspb.2013.2695>.
- Bulla, M., Valcu, M., Dokter, A.M., Dondua, A.G., Kosztolányi, A., Ruten, A., et al., 2016. Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature* 540: 109–113. <https://doi.org/10.1101/084806>.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., et al., 2012. How does climate change cause extinction? *Proc. R. Soc. B* 280 (20121890). <https://doi.org/10.1098/rspb.2012.1890>.
- Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species of climate warming. *Science* 333:1024–1026. <https://doi.org/10.1126/science.1206432>.
- Clement, M.J., Hines, J.E., Nichols, J.D., Pardieck, K.L., Ziolkowski, D.J., 2016. Estimating indices of range shifts in birds using dynamic models when detection is imperfect. *Glob. Chang. Biol.* 22:3273–3285. <https://doi.org/10.1111/gcb.13283>.
- Conklin, J.R., Battley, P.F., Potter, M.A., Fox, J.W., 2010. Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. *Nat. Commun.* 1:67. <https://doi.org/10.1038/ncomms1072>.
- Cruz-McDonnell, K.K., Wolf, B.O., 2016. Rapid warming and drought negatively impact population size and reproductive dynamics of an avian predator in the arid southwest. *Glob. Chang. Biol.* 22:237–253. <https://doi.org/10.1111/gcb.13092>.
- Ge, Q., Wang, H., Rutishauser, T., Dai, J., 2015. Phenological response to climate change in China: a meta-analysis. *Glob. Chang. Biol.* 21:265–274. <https://doi.org/10.1111/gcb.12648>.
- Gillson, L., Dawson, T.P., Jack, S., McGeoch, M.A., 2013. Accommodating climate change contingencies in conservation strategy. *Trends Ecol. Evol.* 28:135–142. <https://doi.org/10.1016/j.tree.2012.10.008>.
- Goodenough, A.E., Hart, A.G., 2013. Correlates of vulnerability to climate-induced distribution changes in European avifauna: habitat, migration and endemism. *Clim. Chang.* 118:659–669. <https://doi.org/10.1007/s10584-012-0688-x>.
- Gordo, O., Sanz, J.J., 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. *Glob. Chang. Biol.* 16:1082–1106. <https://doi.org/10.1111/j.1365-2486.2009.02084.x>.
- Gordo, O., Brotons, L., Ferrer, X., Comas, P., 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Glob. Chang. Biol.* 11:12–21. <https://doi.org/10.1111/j.1365-2486.2004.00875.x>.
- Hausfather, Z., Cowtan, K., Clarke, D.C., Jacobs, P., Richardson, M., Rohde, R., 2017. Assessing recent warming using instrumentally homogeneous sea surface temperature records. *Sci. Adv.* 3, e1601207. <https://doi.org/10.1126/sciadv.1601207>.
- Hethcoat, M.G., Chalfoun, A.D., 2015. Towards a mechanistic understanding of human-induced rapid environmental change: a case study linking energy development, nest predation and predators. *J. Appl. Ecol.* 52:1492–1499. <https://doi.org/10.1111/1365-2664.12513>.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already. *Trends Ecol. Evol.* 15:56–61. <https://doi.org/10.1111/j.1749-4877.2010.00200.x>.
- IGN, 2015. Nomenclator. Instituto Geográfico Nacional, Madrid.
- IPCC, 2014. Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., et al., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526:574–577. <https://doi.org/10.1038/nature15374>.
- Jenouvrier, S., 2013. Impacts of climate change on avian populations. *Glob. Chang. Biol.* 19:2036–2057. <https://doi.org/10.1111/gcb.12195>.
- Jezkova, T., Wiens, J.J., 2016. Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. *Proc. R. Soc. B* 283:20162104. <https://doi.org/10.1098/rspb.2016.2104>.
- Jonzén, N., Hedenström, A., Lundberg, P., 2007. Climate change and the optimal arrival of migratory birds. *Proc. R. Soc. B* 274:269–274. <https://doi.org/10.1098/rspb.2006.3719>.
- Jørgensen, P.S., Böhning-Gaese, K., Thorup, K., Tøttrup, A.P., Chylarecki, P., Jiguet, F., et al., 2016. Continent-scale global change attribution in European birds - combining annual and decadal time scales. *Glob. Chang. Biol.* 22:530–543. <https://doi.org/10.1111/gcb.13097>.
- Knudsen, E., Lindén, A., Ergon, T., Jonzén, N., Vik, J.O., Knappe, J., et al., 2007. Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Clim. Res.* 35:59–77. <https://doi.org/10.3354/cr00714>.
- Kullberg, C., Fransson, T., Hedlund, J., Jonzén, N., Langvall, O., Nilsson, J., et al., 2015. Change in spring arrival of migratory birds under an era of climate change, Swedish data from the last 140 years. *Ambio* 44:69–77. <https://doi.org/10.1007/s13280-014-0600-1>.
- La Sorte, F.A., Fink, D., 2017. Migration distance, ecological barriers and en-route variation in the migratory behaviour of terrestrial bird populations. *Glob. Ecol. Biogeogr.* 26: 216–227. <https://doi.org/10.1111/geb.12534>.
- Langham, G.M., Schuetz, J.G., Distler, T., Soykan, C.U., Wilsey, C., 2015. Conservation status of North American birds in the face of future climate change. *PLoS One* 10, e0135350. <https://doi.org/10.1371/journal.pone.0135350>.
- Lehikoinen, A., Virkkala, R., 2016. North by North-West: climate change and directions of density shifts in birds. *Glob. Chang. Biol.* 22:1121–1129. <https://doi.org/10.1111/gcb.13150>.
- Macmynowski, D.P., Root, T.L., Ballard, G., Geupel, G.R., 2007. Changes in spring arrival of Nearctic–Neotropical migrants attributed to multiscalar climate. *Glob. Chang. Biol.* 13: 2239–2251. <https://doi.org/10.1111/j.1365-2486.2007.01448.x>.
- Madliger, C.L., Love, O.P., 2016. Do baseline glucocorticoids simultaneously represent fitness and environmental quality in a declining aerial insectivore? *Oikos* 125: 1824–1837. <https://doi.org/10.1111/oik.03354>.
- Mariette, M.M., Buchanan, K.L., Buttemer, W.A., Careau, V., 2015. Tough decisions: reproductive timing and output vary with individuals' physiology, behavior and past success in a social opportunistic breeder. *Horm. Behav.* 76:23–33. <https://doi.org/10.1016/j.yhbeh.2015.03.011>.
- Marra, P.P., Studds, C.E., Wilson, S., Sillett, T.S., Sherry, T.W., Holmes, R.T., et al., 2015. Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. *Proc. R. Soc. B* 282:20150624. <https://doi.org/10.1098/rspb.2015.0624>.
- Martin, T.E., Maron, J.L., 2012. Climate impacts on bird and plant communities from altered animal–plant interactions. *Nat. Clim. Chang.* 2:195–200. <https://doi.org/10.1038/nclimate1348>.
- McDermott, M.E., DeGroot, L.W., 2016. Long-term climate impacts on breeding bird phenology in Pennsylvania, USA. *Glob. Chang. Biol.* 22:3304–3319. <https://doi.org/10.1111/gcb.13363>.
- Miller-Rushing, A.J., Lloyd-Evans, T.L., Primack, R.B., Satzing, P., 2008. Bird migration times, climate change, and changing population sizes. *Glob. Chang. Biol.* 14: 1959–1972. <https://doi.org/10.1111/j.1365-2486.2008.01619.x>.
- Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D., et al., 2010. The next generation of scenarios for climate change research and assessment. *Nature* 463:747–756. <https://doi.org/10.1038/nature08823>.
- Ockendon, N., Leech, D., Pearce-Higgins, J.W., 2013. Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. *Biol. Lett.* 9:20130669. <https://doi.org/10.1098/rsbl.2013.0669>.
- Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., et al., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Glob. Chang. Biol.* 20: 2221–2229. <https://doi.org/10.1111/gcb.12559>.
- Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., et al., 2015. Assessing species vulnerability to climate change. *Nat. Clim. Chang.* 5: 215–225. <https://doi.org/10.1038/nclimate2448>.

- Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952–2000 in the Mediterranean region. *Glob. Chang. Biol.* 8:531–544. <https://doi.org/10.1046/j.1365-2486.2002.00489.x>.
- Rivalan, P., Frederiksen, M., Loï, G., Julliard, R., 2007. Contrasting responses of migration strategies in two European thrushes to climate change. *Glob. Chang. Biol.* 13: 275–287. <https://doi.org/10.1111/j.1365-2486.2006.01290.x>.
- Rodríguez-Teijeiro, J.D., Sardà-Palomera, F., Nadal, J., Ferrer, X., Ponz, C., Puigcerver, M., 2009. The effects of mowing and agricultural landscape management on population movements of the Common quail. *J. Biogeogr.* 36:1891–1898. <https://doi.org/10.1111/j.1365-2699.2009.02109.x>.
- Rushing, C.S., Ryder, T.B., Marra, P.P., Rushing, C.S., 2016. Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc. R. Soc. B* 283: 20152846. <https://doi.org/10.1098/rspb.2015.2846>.
- Saino, N., Ambrosini, R., 2008. Climatic connectivity between Africa and Europe may serve as a basis for phenotypic adjustment of migration schedules of trans-Saharan migratory birds. *Glob. Chang. Biol.* 14:250–263. <https://doi.org/10.1111/j.1365-2486.2007.01488.x>.
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., et al., 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc. R. Soc. B* 278:835–842. <https://doi.org/10.1098/rspb.2010.1778>.
- Sanz, J.J., Potti, J., Moreno, J., Merino, S., Frías, O., 2003. Climate change and fitness of a migratory bird breeding in the Mediterranean region. *Glob. Chang. Biol.* 9, 461–472.
- Sardà-Palomera, F., Puigcerver, M., Brotons, L., Rodríguez-Teijeiro, J.D., 2012. Modelling seasonal changes in the distribution of Common Quail *Coturnix coturnix* in farmland landscapes using remote sensing. *Ibis* 154:703–713. <https://doi.org/10.1111/j.1474-919X.2012.01254.x>.
- SAS, 2015. *Fitting Linear Models, JMP® 12 Fitting Linear Models*. SAS Institute Inc., Cary, NC, USA.
- Savo, V., Lepofsky, D., Benner, J.P., Kohfeld, K.E., Bailey, J., Lertzman, K., 2016. Observations of climate change among subsistence-oriented communities around the world. *Nat. Clim. Chang.* 6:462–473. <https://doi.org/10.1038/nclimate2958>.
- Sax, D.F., Early, R., Bellemare, J., 2013. Niche syndromes, species extinction risks, and management under climate change. *Trends Ecol. Evol.* 28:517–523. <https://doi.org/10.1016/j.tree.2013.05.010>.
- Schaefer, H.C., Jetz, W., Böhning-Gaese, K., 2008. Impact of climate change on migratory birds: community reassembly versus adaptation. *Glob. Ecol. Biogeogr.* 17:38–49. <https://doi.org/10.1111/j.1466-8238.2007.00341.x>.
- Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T., et al., 2016. The broad footprint of climate change from genes to biomes to people. *Science* 354:719. <https://doi.org/10.1126/science.aaf7671>.
- Singh, J., Budki, P., Rani, S., Kumar, V., 2012. Temperature alters the photoperiodically controlled phenologies linked with migration and reproduction in a night-migratory songbird. *Proc. R. Soc. B* 279:509–515. <https://doi.org/10.1098/rspb.2011.1062>.
- Small-Lorenz, S.L., Culp, L.A., Ryder, T.B., Will, T.C., Marra, P.P., 2013. A blind spot in climate change vulnerability assessments. *Nat. Clim. Chang.* 3:91–93. <https://doi.org/10.1038/nclimate1810>.
- Snyder, C.W., 2016. Evolution of global temperature over the past two million years. *Nature* 538:226–228. <https://doi.org/10.1038/nature19798>.
- Somveille, M., Rodrigues, A.S.L., Manica, A., 2015. Why do birds migrate? A macroecological perspective. *Glob. Ecol. Biogeogr.* 24:664–674. <https://doi.org/10.1111/geb.12298>.
- Stephens, P.A., Mason, L.R., Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., et al., 2016. Consistent response of bird populations to climate change on two continents. *Science* 352:84–87. <https://doi.org/10.1126/science.aac4858>.
- Studds, C.E., Marra, P.P., 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proc. R. Soc. B* 278:3437–3443. <https://doi.org/10.1098/rspb.2011.0332>.
- Tanner, E.P., Elmore, R.D., Fuhlendorf, S.D., Davis, C.A., Dahlgren, D.K., Orange, J.P., 2017. Extreme climatic events constrain space use and survival of a ground-nesting bird. *Glob. Chang. Biol.* 23:1832–1846. <https://doi.org/10.1111/gcb.13505>.
- Taylor, C.M., Laughlin, A.J., Hall, R.J., 2016. The response of migratory populations to phenological change: a Migratory Flow Network modelling approach. *J. Anim. Ecol.* 85: 648–659. <https://doi.org/10.1111/1365-2656.12494>.
- Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega, M.L., et al., 2017. Resource tracking within and across continents in long-distance bird migrants. *Sci. Adv.* 3, e1601360. <https://doi.org/10.1126/sciadv.1601360>.
- Tierney, J.E., Pausata, F.S.R., DeMenocal, P.B., 2017. Rainfall regimes of the Green Sahara. *Sci. Adv.* 3, e1601503. <https://doi.org/10.1126/sciadv.1601503>.
- Urban, M.C., 2015. Climate change. *Science* 348:571–573. <https://doi.org/10.1126/science.aaa4984>.
- Visser, M.E., Both, C., 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B* 272:2561–2569. <https://doi.org/10.1098/rspb.2005.3356>.
- Wade, A.A., Hand, B.K., Kovach, R.P., Luikart, G., Whited, D.C., Muhlfeld, C.C., 2017. Accounting for adaptive capacity and uncertainty in assessments of species' climate-change vulnerability. *Conserv. Biol.* 31:136–149. <https://doi.org/10.1111/cobi.12764>.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci.* 106:19729–19736. <https://doi.org/10.1073/pnas.0901639106>.
- Wilson, A.M., Jetz, W., 2016. Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. *PLoS Biol.* 14, e1002415. <https://doi.org/10.1371/journal.pbio.1002415>.
- Zhang, X., Lohmann, G., Knorr, G., Purcell, C., 2014. Abrupt glacial climate shifts controlled by ice sheet changes. *Nature* 512:290–294. <https://doi.org/10.1038/nature13592>.
- Zuckerberg, B., Fink, D., La Sorte, F.A., Hochachka, W.M., Kelling, S., 2016. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. *Divers. Distrib.* 22:717–730. <https://doi.org/10.1111/ddi.12428>.