The end of primary moult as an indicator of global warming effects in the Red-legged Partridge *Alectoris rufa*, a medium sized, sedentary species

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ARTICLE INFO

ABSTRACT

Global warming affects ecosystem services, communities and populations, influencing the physiology, behaviour or environment of living beings, and hence impacts its survival or breeding. Identifying species susceptibility to warming is relevant in assessing risks to animal populations and ecological processes. The progressive increase in ambient temperature as a result of global warming might have an effect on the timing of primary moult. This could affect a bird's annual cycle, influencing reproductive success and population dynamics.

We describe a method to examine the potential effects of global warming on the primary moult process in a sedentary population of Red-legged Partridges (*Alectoris rufa*). We organised the factors that might influence the timing of moult end into a network and distinguished between environmental and intrinsic factors. We sorted the factors according to their contribution to quantitative moult models and constructed a diagrammatic scheme showing their interactions and effect on the end of primary moult over the annual cycle.

In Red-legged Partridges, the timing of the end of moult varies according to age-sex class. We found no timing differences by age, but found significant timing differences by adult sex. More females overlap their moult with juveniles than males because female parental effort is higher, more females incubate and brood chicks. The timing of the end of moult varies by year due to conspecific interactions that change according to influences of the weather, habitat, and social and flock conditions. Parent birds synchronize their primary moult with the chick's growth, degree of cover and food resources. From the time of hatching to the following year, the date (day-length), social factors (conspecific interactions), and weather (resources) affect the timing of moult and the birds' annual cycle.

Global warming affects the timing of the end of moult and that of the annual cycle. If the extent of the breeding period is shortened, there could be a negative effect on population outcomes. Middle size prey species are key in trophic chains. Our results suggest that the timing of the end of moult could be used as a proxy measure of warming impacts on wildlife and ecosystems and also as a tool for the management of game birds.

1. Introduction

Anthropogenic climate change is increasingly threatening ecosystems and species worldwide. Warming affect biodiversity at a global scale by modifying species distributions, population dynamics and altering their habitats, contributing to biodiversity loss (Brambilla et al., 2018; Jetz et al., 2007; Powers and Jetz, 2019). However, local extinction of species can occur with a substantial delay following habitat loss or degradation. The consequences of warming on biodiversity might be underestimated (Kuussaari et al., 2009). Most of this decline being attributed to more common species that have greater importance in terms of ecosystem function and service provision (Inger et al., 2015). Disentangling climatic impact on other factors can be difficult. Warming may limit species' distributions directly, but in other cases the link to warming may be mediated by biotic interactions. The principal warming change related threats to populations may come from altered species interactions, providing an early indication of range contractions and population declines (Ockendon et al., 2014).

Feathers become worn over time and their renewal is necessary for flight, insulation, communication and camouflage (Kiat and Izhaki,

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2016; Jenni and Winkler, 2020). In passerines, the relative timing of the different types of moult, and other events in the annual cycle, are affected by global warming (Socolar et al., 2017). In consequence, the length of time taken for the post-juvenile moult has increased and the timing of adult moult has advanced (Helm et al., 2019). However, the effects of climate change on moult at the population level and on population dynamics are largely unknown (Knudsen et al., 2011). Feathers make up 30% of the protein dry mass of a bird's body (Weber et al., 2010), so that moult has a critical effect on avian annual cycles, through the high energy demand that it imposes during several months each year (Ginn and Melville, 1983; Tonra and Reudink, 2018). However, the causes, mechanisms, patterns, and consequences of the primary moult process are still poorly understood (Kiat et al., 2019a).

It is vital for birds to maintain their plumage in good condition and to ensure that its renewal through moult occurs at the best time in a species' annual cycle (Møller and Nielsen, 2018). Moult varies widely in timing, duration, and its degree of overlap with breeding and migration (Jenni and Winkler, 2020). The energetic cost of moult may represent up to 20% of daily energy expenditure and may result in a body mass loss of up to 22% over the course of a full moult (Marmillot et al., 2016). Accordingly, the renewal of the feathers has nutritional requirements similar to the growth of chicks, and this integumentary structure needs an abundant supply of dietary protein (Danner et al., 2015; Le Tortorec et al., 2012).

The moult speed (e.g. the rate of feather renewal), depends on adequate food resources. Moult strategies are shaped by the timing of suitable habitat availability which can provide energy surpluses (protein food), and by the scheduling of reproduction, migration and day-length (Kiat et al., 2016). The moult strategy is a system of mechanisms that schedule the overlap or separation between moult, breeding and migration phases, and which optimize the replacement of feather tracts within the annual cycle according to a bird's life history (Barta et al., 2006; Newton, 2009).

The process of primary moult constitutes a cycle of new feather production. In small birds, this happens once, or perhaps twice, each year, although in large birds it can extend over several years (Rohwer et al., 2009). Flight-feather moult affects minimum daily heart rate, which restricts the capacity of birds to forage and escape predation (Portugal et al., 2018). In sedentary galliform birds, adult primary feather moult overlaps with breeding and both processes (moult and breeding) require sufficient protein food and suitable habitat safe from predators (Demongin, 2016; Pap et al., 2015).

Here, we present a methodological protocol for analysing the end of primary feather moult in the Red-legged Partridge. This procedure helps us to understand the annual timing of population processes and thus interpret the importance of moult in the annual cycle of birds and its implications for conservation (Barta et al., 2006; Brambilla et al., 2018). Bird moult as an ecological indicator is embedded in environmental management, sustainable development and biodiversity conservation (Butler et al., 2012). Birds are frequently used as ecological indicators because they are sensitive to changes in habitat quality, pollution, and warming (Canterbury et al., 2000). We have benefited from a long-term 14 year study of a wild population of partridges, a sedentary gamebird living in optimal habitat conditions (Nadal et al., 2016), as a case study. We focus on testing a hypothesis regarding the relative contribution of factors that affect the end of moult. Our goal is to provide a study protocol to understand the timing of the end of moult and assess the consequences of global warming on wildlife.

2. Material and methods

2.1. The study species

The Red-legged Partridge is a ground-dwelling species native to Mediterranean habitats. It is sexually size-dimorphic, males being larger than females (Nadal et al., 2018a). It is a key prey and small-game
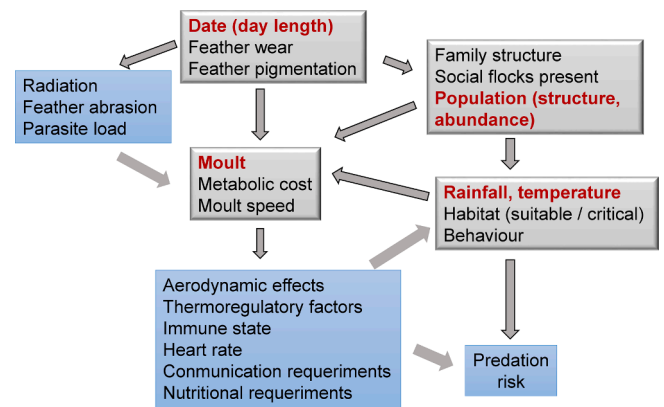

Fig. 1. Diagram of the nomological network showing the interrelationships between the causes, explanatory variables and consequences of factors on the timing of the end of primary moult. Those used in the Generalized Linear Models (GLMs) are shown in red. The rainfall-habitat-behaviour box has direct, indirect and bidirectional relationships. The highlighted boxes and arrows are studied.

species that employs a social strategy (flocking) to maximize its foraging efficiency and to defend itself against predators. Pair bonds form when winter flocks break up. Partridges build their nests and females lay their eggs in April (average clutch size 11.4). The eggs hatch after 23 days of incubation (41% of males incubated a clutch on their own (Casas et al., 2009). The raising of chicks begins in June. Chicks are precocial and grow rapidly. They make short flights after two weeks, and reach adult size after three months. At four and a half months of age they have completed the juvenile moult (Nadal et al., 2018b). Adults begin to moult their primaries while breeding (in late June–late August) and complete this when breeding has finished (in late August to mid-November), but the precise relationship between the moult of adults and their chicks is unknown (Ginn and Melville, 1983).

2.2. Study area

Las Ensanchas is a small-game hunting ground in the Jabalón River basin in Ciudad Real, Spain (38°39′ N, 3°13′ W, 790–840 m a.s.l.). The landscape is Mediterranean Dehesa including a mosaic of cereal crops, fallow, natural pastures (75%) and scrubland (25%) with scattered holm oaks (*Quercus ilex*). The habitat structure remained constant during the study period (1998–2011), and the abundance of resources varied with the annual weather conditions (for details see Nadal et al., 2016).

2.3. Hypothesis generation

We defined a general theory for primary moult in sedentary, medium-sized birds and a specific model of primary moult for the genus *Alectoris* (Nadal et al., 2018c). We selected a pool of easily measurable factors that affect moult (environmental and intrinsic) and constructed a nomological network to order them (Hughes, 2000). We arranged the factors diagrammatically according to their interrelationships and their driver effects (Fig. 1). As environmental factors we considered: 1) the date; 2) the temperature; and 3) the rainfall. As intrinsic factors we considered: 1) the autumn population size; 2) the number of adults; 3) the number of juveniles; 4) the population age-ratio; 5) the population sex-ratio; 6) the juvenile sex-ratio; and 7) the adult sex-ratio (Alfaro et al., 2018; De la Hera et al., 2010; Dietz et al., 2015; Pol et al., 2016). We used the network of factors to formulate hypotheses, following the chain of logical consequences. We created: a) causal hypotheses to explain how each factor might affect the timing of the end of moult (e.g. that the date [day length] triggers the end of moult); b) functional hypotheses to explain the role of factor change on the end of moult (e.g. that the end of moult implies less secretive predator avoidance

behaviour); c) generalizing hypotheses to describe an observed pattern on the end of moult (e.g. that the end of moult of females and young overlaps) and; d) explanatory hypotheses to provide reasons to generalize the factor effect on the end of moult (e.g. that population structure and warming [environment] modify the timing of moult because birds need to account for the metabolic cost of moult). We also considered alternative hypotheses to provide other arguments for the previous hypotheses (e.g. that population structure and warming [environment] modify the timing of moult because birds need to minimise predation risk) (Buttemer et al., 2019; Franklin et al., 2017; Hanć et al., 2017; Jahn et al., 2016). We hypothesised that warming affects environmental resources and so advances the timing of the end of moult (Tomotani et al., 2018b). This would decrease population productivity and could drive the population into progressive decline (Martin et al., 2018; Visser et al., 2011).

2.4. Data collection

We studied wild partridges collected during hunts performed from mid-October to mid-November, between 1998 and 2011. We determined bird age by examining the primary feathers, and sex by spur characteristics. We cut through the ulna-radius to remove a wing from each bird and dried them for 15 days at 40 °C in the laboratory. We recorded feathers-length from the wing-tip to the insertion of the 8th, 9th and 10th primary feathers into the integument, all to the nearest 0.5 mm (Nadal et al., 2016). Each bird was classified as in are moulting or finish moult.

We used data from the Las Terceras and Torrenueva meteorological stations run by AEMET (the Spanish Meteorological Agency, http://www.aemet.es) located at 300 m and 12 km from the study area, respectively. To assess annual variations in temperature, we used data from the Torrenueva meteorological station, because it has a more consistent long-term data series. To study the yearly effects of meteorology on moult, we selected the January–September period for rainfall and April–September for temperature (Halbritter et al., 2020).

2.5. Procedure for the moult study and hypothesis verification

First, we visualised the main data in graphic form to build a conceptual model for the end of primary moult (Moreno-Palacios et al., 2018). The end of the moult occurs towards the end of October, when the number of partridges moulting decreases. The maximum hatching happens 130 days before, in the month of June (Nadal et al., 2016). For juveniles and adults to synchronize at the end of the primary moult, juveniles must begin moulting 30 days after hatching and adults when chicks are born.

We selected and ordered the hypotheses from the particular to the general. We chose independent factors that are easily measurable. We sorted the key factors driving the end of moult depending on their contribution to different Generalized Linear Models (GLMs). To determine the association between factors, we analysed them at two levels, between and within all age and sex groups (Kiat and Sapir, 2017). We examined the following hypotheses: 1) that more adult females than adult males synchronize their moult with juveniles, because of their higher parental effort during incubation and chick-rearing (Cockburn, 2006); 2) that juveniles and adults align their primary renewal to foster social cohesion, so that they can feed without being predated (Møller and Nielsen, 2018); 3) that weather affects environment seasonality (resource scheduler) and individuals influence their social group, so that both date and social interactions can modify the end of moult (Jukema and Wiersma, 2014); and 4) that warming varies the environment seasonality that drives the annual ecological cycle (Mason et al., 2019).

The aim was to see whether the date of the end of a birds' moult can be used as a proxy to measure the effect of warming on this species, and other species by extension (Kiat et al., 2019b; Podlaszczuk et al., 2016; Weeks et al., 2020). We developed a conceptual model of the primary
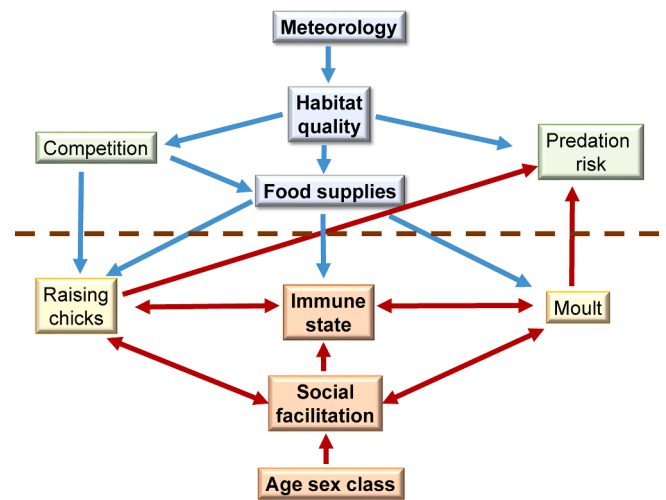

Fig. 2. A proposed conceptual model explaining how environmental (blue arrows) and intrinsic factors (red arrows) could affect the timing of the end of moult. Meteorology modulates the annual cycle of habitat resources. Competition, predation, and food availability have effects on the immune state, moult and rearing of chicks. Age and sex class determine social influences and their integration in the group (social facilitation). The immune state, chick rearing and moult are intrinsic factors; competition, food supply and predation risk are environmental factors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
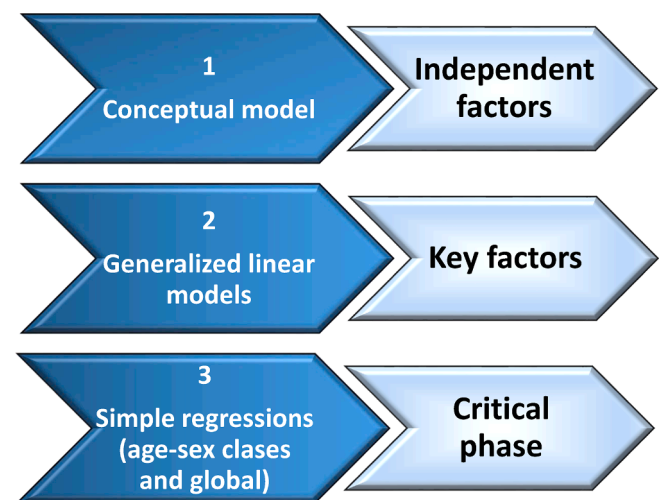

Fig. 3. The three steps in the procedure. First, a conceptual model based on a nomological network is used to select independent factors that affect moult. Second, Generalized Linear Models (GLMs) are performed with different data aggregations to sort key factors. Third, simple regression models are performed using key factors to determine the effects on the timing of the end of primary moult.

renewal of partridges that is driven by environmental and intrinsic factors (Fig. 2) (Ben-Hamo et al., 2017; Visser and Gienapp, 2019). Our method has three steps: first, build a conceptual model (nomological network), second, sort the key factors by relevance, and third, explain the species' annual ecology (Fig. 3).

2.6. Statistical analyses

We performed chi-squared tests on our contingency tables to assess moult differences (moulting or finished moult) between sexes, ages, classes, years, and classes and years. To detect changes in moult over time, we compared each year using an analysis of means for the
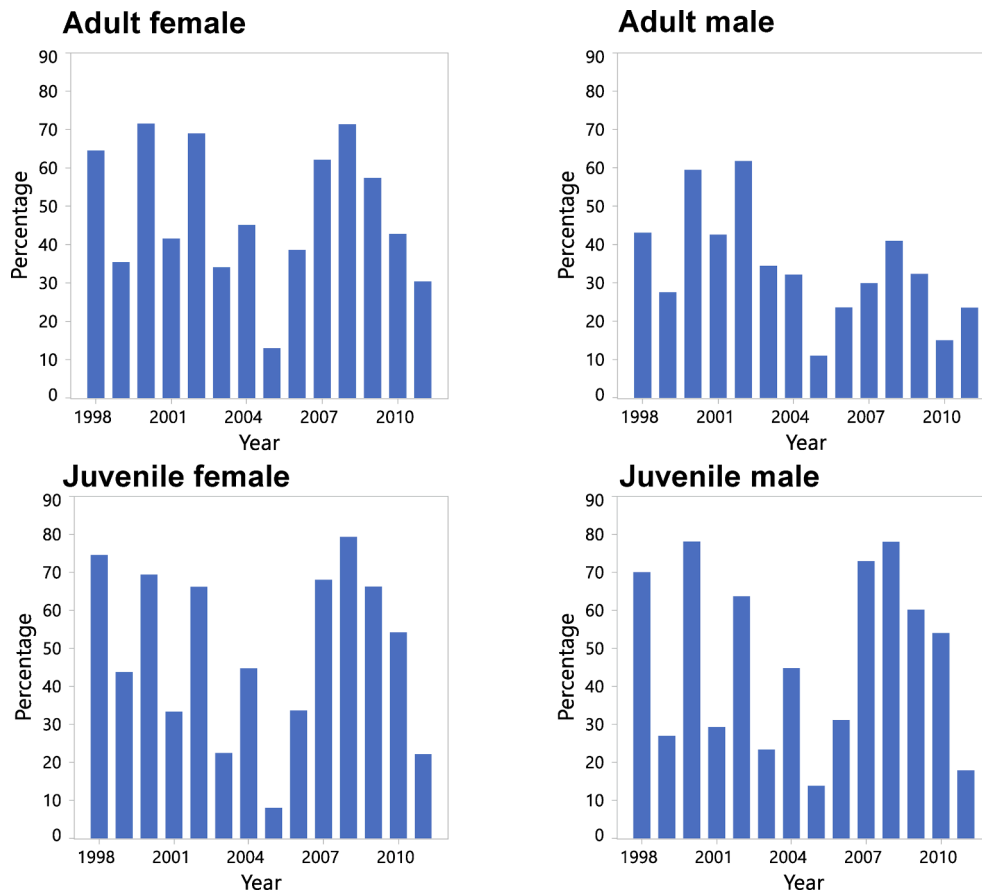
Fig. 4. The percentage of the different age-sex classes moulting between mid-October to mid-November according to age-sex class by year in the Red-legged Partridge.

proportions of denominators by age-sex classes (Supplementary Material 1). We used GLMs to select an environment (date and meteorological) and intrinsic (population) explanatory factors with the greatest contribution in: (a) age-sex classes; (b) age or sex groups; and (c) overall data for all of the partridges. The GLMs used to explain the end of moult were performed with a binomial distribution (moulting or finished moult) and logit as a link function. We used the log of worth (utility) of each explanatory factor in all models vs the other variables to build a rank order of their level of contribution (see Supplementary Material 3). We performed simple regression models with the selected explanatory factors for age-sex class and for overall partridge data. We used JMP14 (SAS Institute Inc, 2018) for all of these statistical analyses.

3. Results

The end of moult differed between the sexes, males finishing earlier than females ($\chi^2_1 = 267$, P < 0.001, N = 12,975, Supplementary Material 1). There were no such differences with respect to age groups (juveniles vs adults) ($X^2_1 = 0.36$, P > 0.55, N = 12,975), although the completion of moult did vary between different age-sex classes ($X^2_3 = 486$, P < 0.001, N = 12,975). The end of moult varied significantly between years ($X^2_{13} = 1342$, P < 0.001, N = 12,975). In 42.8% of years, the date of the end of juvenile female moult differed from that of the mean for all age-sex classes. This percentage increased to 57.1% in the case of juvenile males, 64.3% in the case of adult males, and 85.7% in the case of adult

Table 1
GLMs for the end date of moult: total partridge data, adult, juvenile, and the various age-sex classes.

Model	P	Pearson Goodness of fit test	AICc	1	2	3	4	5	6	7	8	9	N	K
Total	<0.0001	0.06	15,052	Date[4]	Class[4]	SR[4]	Age r[4]	Adul n[4]	Juv n[4]	JSR[4]	Precip[4]	Year[2]	12,975	9
Adult	<0.0001	0.4	7475	Class[4]	Date[4]	SR[4]	Age r[4]	Adul n[4]	Juv n[4]	JSR[4]	Year[1]		6353	8
Juvenile	<0.0001	0.4	7150	Date[4]	SR[4]	Age r[4]	Precip[4]	Juv n[4]	Adul n[4]	Adul n[4]	Year[4]		6622	8
A female	<0.0001	0.7	2840	Date[4]	Juv n[4]	Age r[4]	Year[4]	SR[4]	Adul n[4]	JSR[2]	Tempe[1]		2581	8
A male	<0.0001	0.2	4578	Date[4]	Adul n[4]	SR[4]	Juv n[4]	Year[4]	Age r[2]				3772	6
J female	<0.0001	0.5	3587	Date[4]	SR[4]	Precip[4]	Juv n[4]	Age r[4]	Adul n[4]	JSR[4]	Year[2]		3317	8
J male	<0.0001	0.03	3575	Date[4]	SR[4]	Age r[4]	Precip[4]	Juv n[4]	JSR[4]	Adul n[4]	Year[3]		3305	8

<0.0001 = [4] 0.001 = [3] 0.01 = [2] 0.05 = [1].

Binomial distribution: two plumage categories (a) birds that finish moult (b) birds that are moulting.

Explanatory variables: SR = Sex ratio, ASR = Adult sex ratio, JSR = Juvenile sex ratio, Age r = Age ratio, Preci = Precipitation, Tempe = Temperature, Adult n = Number of adults, Juv n = Number of juveniles.

Models: Total, Adult, Juvenile, A female (Adult female), A male (Adult male), J female (Juvenile female), J male (Juvenile male)..

P = P values for the model, AICc = Corrected Akaike Information Criterion, 1, 2…,9 = Order of the variables in the model according to Log Worth, N = Sample size, K = Number of explanatory variables in the model.

Table 2
Determination coefficients, R^2 below slope $\pm$ SD, of simple regressions for moult between the age-sex classes, and with autumn population size, temperature and the juvenile sex ratio.

	AM	JF	JM	Autumn p	Tempe	JSR
AF	**0.86**[4]	**0.67**[3]	**0.61**[3]	**0.58**[2]	**0.49**[2]	
	0.85 ±	0.69 ±	0.75 ±	0.05 ±	−40.6 ±	
	0.1	0.14	0.17	0.01	12.1	
AM		**0.40**[1]	**0.38**[1]	**0.42**[2]	**0.58**[2]	
		0.58 ±	0.65 ±	0.05 ±	−48.7 ±	
		0.21	0.24	0.02	11.9	
JF			**0.94**[4]	**0.49**[2]		**0.40**[1]
			1.11 ±	0.06 ±		−240 ±
			0.08	0.02		84
JM				**0.49**[2]	**0.35**[1]	**0.29**[1]
				0.04 ±	−35.7 ±	−178 ±
				0.01	14.2	81

$<0.0001 = ^4\ 0.001 = ^3\ 0.01 = ^2\ 0.05 = ^1$.
AF (Adult female), AM (Adult male), JF (Juvenile female), JM (Juvenile male), Autumn p (Autumn population), Tempe (Temperature), JSR (Juvenile sex ratio).

females (Fig. 4, Supplementary Material 2).

Explanatory factors contribute to different utility values of the various GLMs. According to the models, the explanatory factors with the greatest effect on the end of primary moult rank in the order: Date > Sex-ratio > Age-ratio > Adult number > Juvenile number > Precipitation > Year (Table 1, Figs. 1 and 3). In simple regressions, the determination coefficients of moulting birds are higher between juveniles (juvenile female with juvenile male, Table 2) than between adults (adult female with adult male).

In addition, the determination coefficient of the end of moult is higher between adult female and juveniles than between adult male and juveniles. As Table 2 shows, the rest of the associations between the end

of moult of the different age-sex classes with the autumn population size, the temperature, and the juvenile sex-ratio, showed smaller coefficients of determination.

Over the years of the study, we found a progressive increase in the annual average temperature levels ($R^2 = 0.59$; $b = 0.61 \pm 0.08$; N = 46; F = 63.7; $P < 0.0001$). At the end of moult between mid-October and mid-November, the age-sex classes showed associations with temperature, juvenile sex-ratio and autumn population size. According to Fig. 5, the date of the end of moult was earlier as temperature increased ($R^2 = 0.40$; $b = -40.2 \pm 6.9$; N = 56; F = 36; $P < 0.0001$; Fig. 4). The end of moult was also earlier as juvenile sex ratio increased ($R^2 = 0.22$; $b = -164.2 \pm 41.5$; N = 56; F = 15.6; $P < 0.0002$). Moreover the end of moult was later as the autumn population increased ($R^2 = 0.48$; $b = 0.05 \pm 0.007$; N = 56; F = 50.4; $P < 0.0001$).

4. Discussion

Birds are and excellent bio-indicator to understand the effects of warming in animals populations (Jetz et al., 2007). Declines were greatest among those species whose annual productivity was most greatly reduced by asynchrony (Franks et al., 2018). The ecology of different bird species is complex by its diverse life-history traits and ecological relations. Identifying reliable predictors of species resilience or susceptibility to climate warming is critical to assess potential risks to species, communities and ecosystem services (Samplonius et al., 2018).

Primary feather growth is scheduled according to a species' life-history strategy. After hatching, chicks develop the structures of the skin from which the first juvenile plumage will grow. In *Alectoris* species, the post-juvenile moult replaces the juvenile plumage, except for the 9th and 10th primaries, which are retained. Following this, the previous generation of primary remiges is renewed each year (Demongin, 2016; Pyle, 2013). The comparison of moult patterns between different age
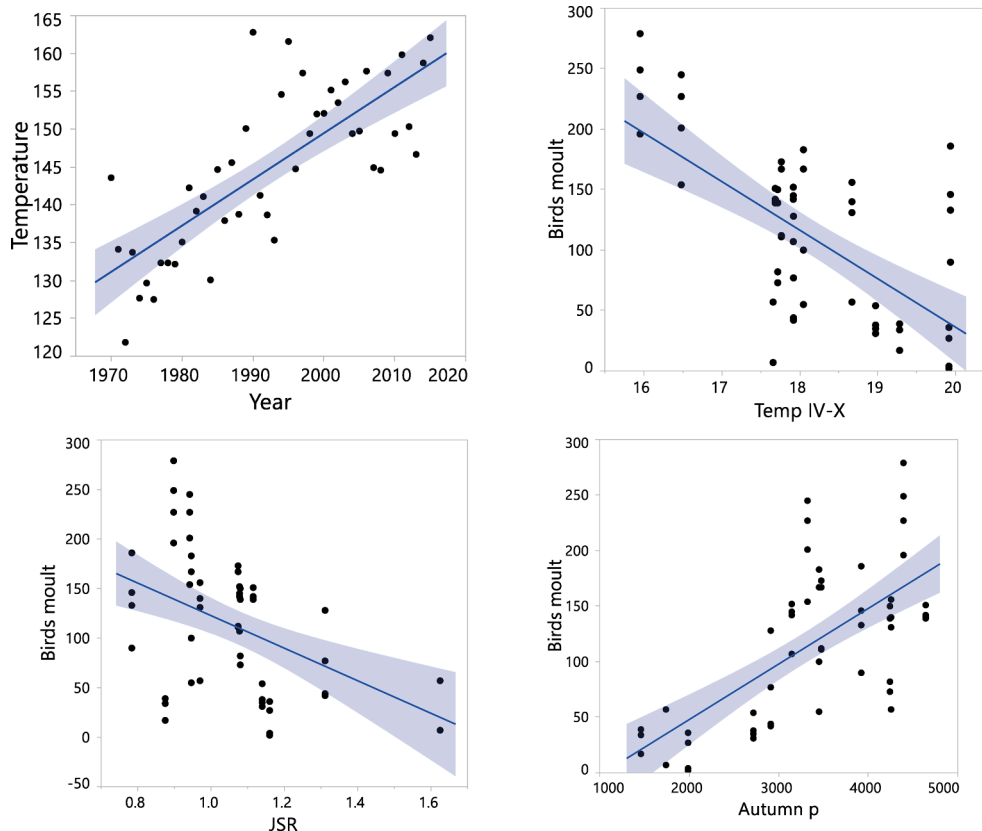

Fig. 5. Birds that moult of age-sex classes in relation to: Mean temperatures during April–October (Temp IV-X), Juvenile sex ratio (JSR), Autumn population size (Autumn p), and between temperature and year.

classes is essential to understand the process (Jahn et al., 2016). Our results show that while juvenile moult relates to adult moult, the end date of these moults is independent (Fig. 4 and Table 2). There is no difference in the date of the end of moult between young and adults, although there is between adult females and adult males (chi-squared tests on contingency tables). The moult of adults depends on the moult of juveniles since adults organize their moult schedule around their breeding activities. In passerines, for example, juvenile moult responds to natural selection and adult moult to sexual selection (Guallar and Jovani, 2019).

Any damage to the primary feathers impairs flight efficiency and hinders escape from predators (Kullberg et al., 1996). This reduction in flight capacity due to moult is compensated by changes in behaviour (Tomotani and Muijres, 2019). Outside the breeding season, Red-legged Partridges live in compact flocks, individuals remaining close to each other while several individuals at a time keep constant watch for danger. In this way, a flock acts in concert to compensate for the reduction in flight capacity during moult. Larger groups are better able to find food while also watching out for predators (Lamb et al., 2019). Group cohesion promotes social interactions and improves a flock's ability to utilise resources and guarantee security from predation. We found that juveniles and adults synchronize their moult (Table 1 and 2). As they grow, chicks devote a lot of time to rest and vigilance, which could enhance the moult process. Growing juveniles need optimal habitat conditions with an abundance of protein food (invertebrates and seeds) and the best height and density of vegetation to hide from predators, thereby reducing the risks associated with limited flight capacity (Kiat and Sapir, 2018). The amount of food and cover available depends on the weather.

Our data show that the end of moult varies by year according to weather and resource availability. During moult, birds combine an environment rich in resources with secretive behaviour to reduce activity, minimise energy expenditure, and lower predation risk (Martin et al., 2018; Panek and Majewski, 1990). Birds also alter their escape flight behaviour to compensate for the reduction in performance when flying with wing gaps (Tomotani et al., 2018a). For example, northern hemisphere waterfowl species moult where the risk of predation is lower, during periods of warmer temperatures and before food supplies and the availability of aquatic habitats approach their winter minima. By contrast, southern hemisphere waterfowl delay the onset of moult until the dry season, opting to moult when both food and aquatic habitats are scarce (Ndlovu et al., 2017b). Moult requires large amounts of nutrients and energy to accommodate various metabolic and physiological changes, as vascularization, blood volume and erythrocyte levels increase (Marmillot et al., 2016). Protein turnover rate increases in birds growing new feathers (Ben-Hamo et al., 2017). The nutritional benefit of habitats rich in protein foods has a strong effect on the timing and location of moulting, and this seasonal constraint places limits on the moult schedule (Kiat and Sapir, 2017; Szép et al., 2019). For example, the speed of flight-feather renewal in insectivorous birds is slightly higher in years with higher rainfall and a greater abundance of insects (Saino et al., 2017). The minimum resting metabolic rate increases over the moult period by up to 40–63% (Buttemer et al., 2019). Intrinsic factors depend on a sufficient food supply which in turn depends on the weather.

Our results show that completion of moult varies widely between: individuals (according to size); age-sex classes (according to biology); social groups (according to behaviour); and years (according to weather). Because of their differing biological characteristics, different age and sex classes have their own requirements, although in the population as a whole they complement each other to gain biological efficiency (Nadal et al., 2018b). In prey species, females generally invest more effort in parental tasks (e.g. incubation and chick-rearing) than males (Cockburn, 2006). In line with our data, the proportion of adult females that synchronize their moult with juveniles is generally higher; females adjust their moult to accommodate the need to find food and accompany their chicks. In raptor species, the timing of adult moult is reversed; adult females moult earlier than adult males (Ramírez and Panuccio, 2019; Zuberogoitia et al., 2018). Flexibility in the timing of moult is widespread in both resident and migratory birds (Rohwer et al., 2011) and the extent of the primary moult varies substantially between species (Rohwer et al., 2009). In juvenile passerines, the duration and advance in timing of moult has increased over the last 212 years, in line with environmental warming (Kiat et al., 2019b). Ecological conditions affect moult and wing morphology (Matloff et al., 2020). Fresh feathers play a role in conspecific and heterospecific interactions, resistance to parasites, natural and sexual selection (Wright et al., 2018), and seasonal behaviour and new annual cycle stages often follow periods of moult.

Moult strategies, the timing and overlaps of moult and other activities, vary between sedentary and migratory birds, and also with latitude. Sedentary and short-distance migrants normally overlap breeding and moult, while long-distance migrants exhibit more than eight different moult strategies (Newton, 2009). Migratory species may perform partial primary moults, suspending moult once a certain feather series has been renewed, and delaying moult of the remaining feathers until arrival in the winter quarters (Tonra and Reudink, 2018). Waterfowl are flightless during moult and face associated risks in stopover/staging areas (Ndlovu et al., 2017a). Our results show that overlap between breeding and moult favour synchrony in the moult of adults and young. Some species appear to avoid overlapping active migration with moult and perform either rapid and shorter, or slower and more protracted moults. Others overlap moult and migration, performing a slow, continuous moult depending on migration distance and duration (Ginn and Melville, 1983). Different fluctuations in body mass and pectoral muscle size during flight-feather moult are associated with interspecific differences in their moult strategy (Ndlovu et al., 2017a).

Eighty per cent of passerines in tropical areas exhibit moult-breeding overlap, and compensate by growing new feathers slowly (Echeverry-Galvis and Hau, 2013). Moult while breeding may be more common in larger species because the length of the reproductive period, as well as the time required to replace large flight-feathers, increases with body size (Rohwer et al., 2009; Jenni et al., 2020). Moult-breeding overlap is a common strategy in precocial and sedentary birds, which can take advantage of abundant protein foods and plenty of vegetation cover to minimize the impact of predation and therefore can synchronise seasonality (time) with habitat quality (resources) (Szép et al., 2019). According to our results, *Alectoris* species synchronise shedding and growth of primary feathers in juveniles and adults (Tables 1 and 2, Supplementary Material 2). Flight-feather growth patterns develop early during embryogenesis, much earlier than for other feather types (Kondo et al., 2018). Our results show that moult lasts for 100 days in chicks and 130 days in adults and that chicks begin moult 30 days after hatching, thereby synchronising the end of their moult with adults (Fig. 4). In the Common Ground Dove *Columbina passerina* (an altricial species) juveniles usually have more than two adjacent feathers growing simultaneously, and replace their primaries in about 100 days. In contrast, adults, which overlap moult and breeding extensively, usually grow just a single primary at a time and take at least 145 days to replace all of their primaries (Rohwer and Rohwer, 2018).

The date of moult changes each year because it fits with reproduction, which is timed to vegetation growth and cereal (food) ripening which in turn depends on the weather conditions and seasonality of the year in question. Our results suggest that date and social interactions can also change the timing of moult (Supplementary Material 1). The end of primary moult generally matches the end of breeding and gives way to the beginning of a new cycle for the population (Mettke-Hofmann et al., 2010). Seeds germinate with the autumn rain and new growth covers the soil, bringing food for partridges. After the moult, the birds acquire critical pigments essential for intraspecific interactions (Mcgraw et al., 2006; Reudink et al., 2009) and ectoparasite resistance (Gunderson et al., 2008). After wintering in a flock, partridges begin pair formation
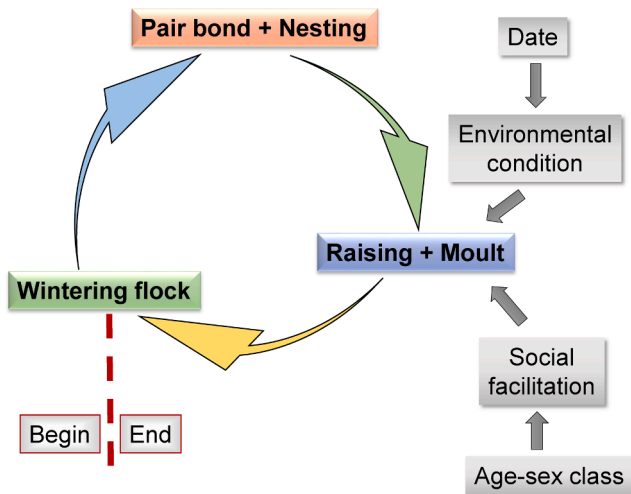
Fig. 6. Conceptual model explaining the moult process.

and then enter the nesting period. Primary moult begins in adults during the hatching period, while in chicks it occurs just one month after hatching (Fig. 4, Table 2). The weather generally depends on date and drives habitat characteristics and phenology, which in turn modulate the moult. Furthermore, the age and sex class affect social cohesion, which in turn modulates the moult (Fig. 6).

Bird moult advances with global warming probably because warming advances seasonality, which drives the timing of the biological cycle (Miller-Rushing et al., 2010). Sedentary birds such as the Red-legged Partridge provide useful comparisons of warming effects between years. This contrasts with migratory species that divide their annual cycle between different geographical regions and are therefore more difficult to understand in relation to global warming. The mobile species can change their location to better habitats according to shifts in the timing of seasonal conditions, and so ameliorate the effects of warming (Samplonius et al., 2018). In the hottest years, breeding and moult end early, and so could reduce reproductive success (Fig. 5). Warming causes birds to moult earlier (breeding period decreases) as the juvenile sex ratio increases, and so could lead to population decline (Visser and Gienapp, 2019). Conversely, when moult is delayed, the autumn population increases. This downward trend in population productivity will continue as temperatures continue to rise progressively year on year. We can therefore use the monitoring of a bird's moult timing to assess the impacts of warming on wildlife, and assess the resulting effects on ecological processes and ecosystem services (Inger et al., 2015).

5. Authors' contributions

J.N. designed the study; J.N. and C.P. carried out the field work and analyzed the data. C.P. performed the laboratory analyses; J.N. and A.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

The authors declare to be accountable for the aspects of the work that they conducted and ensuring that questions related to the accuracy or integrity of any part of their work are appropriately investigated and resolved.

6. Ethics approval and consent to participate

The study was conducted in full compliance with Spanish laws and regulations, including a licence from "Las Ensanchas" to sample shot partridges. The protocol was approved by the Committee on the Ethics of Animal Experiments of the University of Lleida (Ref.1998–2012/05).

7. Data Availability

Data are available on request to authors

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107287.

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